

GENETIC STRUCTURE AND GENE FLOW BARRIERS AMONG POPULATIONS OF
AN ALPINE BUMBLE BEE (*BOMBUS BALTEATUS*) IN THE CENTRAL ROCKY
MOUNTAINS

A Thesis
by
KAITLYN MARIE WHITLEY

Submitted to the Graduate School
at Appalachian State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

December 2018
Department of Biology

GENETIC STRUCTURE AND GENE FLOW BARRIERS AMONG POPULATIONS OF
AN ALPINE BUMBLE BEE (*BOMBUS BALTEATUS*) IN THE CENTRAL ROCKY
MOUNTAINS

A Thesis
by
KAITLYN MARIE WHITLEY
December 2018

APPROVED BY:

Jennifer C. Geib, Ph.D.
Chairperson, Thesis Committee

Matt C. Estep, Ph.D.
Member, Thesis Committee

Michael D. Madritch, Ph.D.
Member, Thesis Committee

Zack E. Murrell, Ph.D.
Chairperson, Department of Biology

Michael J. McKenzie, Ph.D.
Dean, Cratis D. Williams School of Graduate Studies

Copyright by Kaitlyn Marie Whitley 2018
All Rights Reserved

Abstract

GENETIC STRUCTURE AND GENE FLOW BARRIERS AMONG POPULATIONS OF AN ALPINE BUMBLE BEE (*BOMBUS BALTEATUS*) IN THE CENTRAL ROCKY MOUNTAINS

Kaitlyn Marie Whitley
B.A., University of North Carolina at Chapel Hill
M.S., Appalachian State University

Chairperson: Dr. Jennifer C. Geib

The intermountain Western US has experienced significant environmental impacts from climate change over the last 50 years, creating novel challenges for species that occupy this area. Metapopulation theory predicts that extant populations with greater interconnection via dispersal and gene flow should be more likely to withstand such environmental challenges, exhibiting greater likelihood of persistence. This study investigated the relative extent of genetic connectance among populations of *Bombus balteatus*, an ecologically important native bumble bee species in alpine habitats of the central Rocky Mountains in Colorado. This species and one other (*B. sylvicola*) historically comprised over 95% of samples captured in the region during the 1960s and 70s but has experienced declines in its relative abundance in recent years. This decline has likely been facilitated by climate-mediated decreases in floral resources coupled with increased competition from upwardly mobile lowland *Bombus* species. I examined population genetic structure using microsatellite markers and then used geospatial modeling to determine how the landscape influences this genetic structure. I used MaxEnt to develop environmental niche models and estimate habitat suitability using climate and landscape data and a

comprehensive set of occurrence records for *B. balteatus*. I used Circuitscape to develop models of habitat connectivity, represented as dispersal pathways between populations and areas of suitable habitat. I also used Circuitscape to estimate pairwise resistance distances between sampling localities in order to examine patterns of Isolation by Resistance among populations.

My data suggest that populations of *B. balteatus* have low but significant pairwise genetic differentiation between populations, with evidence of inbreeding likely due to a heterozygote deficiency, which may be a result of evident population structuring. Structure analyses revealed six genetic clusters among the nine populations sampled, with two clearly defined population groups. Populations did not show isolation by distance and the relationship to pairwise genetic differentiation did not improve by incorporating climate and landscape variables into models as pairwise resistance distances. MaxEnt analyses revealed elevation, land-use, and mean temperature of the wettest quarter as having the strongest influence on the best-fitting niche models. High habitat suitability for *B. balteatus* was predicted to occur at high elevations in areas with high perennial snow and ice. Circuitscape analyses revealed high habitat connectivity along high elevation ridgelines, while dispersal appears to be limited by low elevation forested valleys and major highways. Results suggest that there may not be direct barriers to gene flow and that the current arrangement of suitable habitat at a broad scale may sufficiently explain the observed levels of population differentiation. Although the data suggest populations of *B. balteatus* may be able to disperse across the landscape and exchange genes among populations, conservation management strategies should be directed toward protecting areas of high elevation suitable habitat that connect populations via dispersal pathways.

Acknowledgments

I would like to first and foremost thank Dr. Jennifer Geib for her assistance in all aspects of this study and for her continuing encouragement and support of my research efforts. I would also like to thank my committee members Dr. Matt Estep and Dr. Mike Madritch for their invaluable input and assistance in developing this thesis. I am eternally grateful for Eric Rayfield for his help with experimental design and guidance throughout this project. I am thankful for Isabel Sullivan, Julia Jones, Jacqueline Staab, William Vannoy, Melanie McMillan, Chloé Prunet, and Lucas Piedrahita for providing essential field and laboratory assistance in this project. Finally, I would like to thank my family for their unwavering encouragement and support throughout this process. To my parents, Jeff and Sharon Whitley, thank you for guiding and supporting me unconditionally through this chapter of my life and all of the others. To my twin sister, Lauren Whitley, thank you for always pushing me to stay focused and motivated and to achieve my goals even while attaining your own (you are a superwoman). And lastly, to my grandparents, Carl and Mary Rueger, thank you for showing me what love looks like and thank you for providing me the means to achieve this goal. Funding for this research was provided by Sigma Xi, the Appalachian State University Office of Student Research, and the Wayne Richardson Memorial.

Table of Contents

Abstract	iv
Acknowledgments.....	vi
Foreword	viii
Chapter 1: General Introduction	1
Figures Legend.....	16
Figures.....	17
Chapter 2: Genetic structure and gene flow barriers among populations of an alpine bumble bee (<i>Bombus balteatus</i>) in the central Rocky Mountains	18
Introduction.....	18
Methods.....	21
Results.....	33
Discussion	42
Tables	53
Figure Legends.....	64
Figures.....	66
References cited	76
Appendix A: Summer 2017 Field Collections.....	93
Appendix B: Supplementary Tables and Figures	125
Vita.....	138

Foreword

This work was completed in collaboration with a fellow student, undergraduate Isabel Sullivan, in order to better understand how a heterogeneous landscape influences alpine bumble bees in the central Rocky Mountains. The format and references follow that of the *Journal of Conservation Genetics*.

Chapter 1

GENERAL INTRODUCTION

Pollinators are responsible for facilitating nearly 90% of all flowering plant species reproduction and for increasing the quantity and quality of over 60% of the worlds crops (Jha and Kremen 2013). Bees are one of the most important and effective pollinators and bumble bees are considered keystone species within plant-pollinator communities because they pollinate both abundant and rare plant species (Jha and Kremen 2013). Bumble bees have faced significant declines in relative abundance and geographic range over the past few decades (Cameron et al. 2010). These widespread patterns of decline are largely attributed to habitat fragmentation and loss, agricultural intensification, pathogens and diseases, competition with non-native species, and increased use of pesticides and insecticides (Darvill et al. 2006, Cameron et al. 2010; Hadley and Betts 2012; Dreier et al. 2014).

Bumble bees face many threats in human and climate-altered landscapes and are often the first bee species to be extirpated with land use intensification (Goulson et al. 2008; Jha and Kremen 2013). Bumble bees are particularly susceptible to decline due to their low effective population sizes, low genetic variation from haplo-diploidy, and their monoandrous mating system (Darvill et al. 2006). Although colonies can contain upwards of 200 workers, only one reproductive queen is responsible for producing all the offspring, meaning that even apparently abundant populations may actually have limited genetic diversity and may be more vulnerable to stochastic effects (Dreier et al. 2014).

Bumble bee life cycle

Bumble bees are an ephemeral species; the female workers and male drones typically live for 2-5 weeks while the queens live for 9-12 months (Goulson 2010). Although bumble bees have a fast generation time and are able to evolve quickly (e.g., see Miller-Struttmann et al. 2015), they are also more susceptible to genetic drift because the population is re-established every year. Their life cycle (Fig. 1) begins in the spring, when the queens that have been hibernating over winter emerge as ground temperatures rise (Goulson 2010). These new queens were inseminated the previous year and overwinter with sperm inside of their spermatheca (Goulson 2010). The new queens immediately begin to forage for nectar to regain energy and begin to look for suitable nesting sites to lay their first brood of eggs. This is the first opportunity for dispersal and a new queen can disperse around 1 kilometer away from her overwintering site to found her own colony (Bowers 1985). Because a new queen is inseminated the season before hibernation, she is dispersing male genes as well as her own via the stored sperm and therefore contributes more to gene dispersal than do males (Drier et al. 2014).

Upon finding a suitable nesting site, the first brood a queen lays are all female workers. These workers will help collect pollen and nectar for the colony, while the queen is the sole member responsible for producing more female offspring throughout the season to build the colony (Goulson 2010). As the season comes to an end (the length of which is species-specific) and when both provisions and the colony are abundant in size, the queen will begin producing new queens and males. New queens are produced by receiving more resources over a longer period of time than worker females and males are produced from unfertilized eggs (Goulson 2010). A queen controls the sex of her offspring and can produce

male offspring even when she has not mated, which contributes to the haplodiploid nature of bumble bees (Goulson 2010).

The new queens and males leave the nest to mate with other bumble bees and this is the second opportunity for dispersal. They are the only reproductive members of the colony so their ability to disperse away from their natal site to avoid inbreeding is critical for the success of future colonies (Goulson 2010). Evidence from agricultural habitats suggest that new queens can disperse up to 3-5 km away from their natal colony to mate while males can disperse anywhere from 1-10 km, which helps prevent inbreeding (Lepais et al. 2010; Goulson et al. 2010). Once mated, new queens feed heavily on pollen and nectar to store as energy reserves for hibernation and then search for overwintering sites, which is the final potential for dispersal. The old queen, workers, and males will all die at the end of the season while the new queens survive until the following spring and the cycle begins again (Goulson 2010).

Bumble bee dispersal

Dispersal across landscapes is essential for gene flow, maintaining adaptive genetic variation, and preventing inbreeding (Jha and Kremen 2013). Patterns of dispersal and gene flow are key determinants of a species' ability to respond to population pressures, yet this has been scarcely investigated at a fine scale in bumble bees (Dreier et al. 2014). Very little is known about bumble bee gene flow processes and despite the relevance of dispersal to ecology and conservation, few studies have examined bumble bee dispersal at local spatial scales across heterogeneous landscapes (Jha and Kremen 2013; but see Lozier et al. 2013).

Studies of bumble bee dispersal have typically taken place in agricultural landscapes (Drier et al. 2014), in manipulated landscapes (Goverde et al. 2002; Carvell et al. 2012), or in

island systems (Darvill et al. 2010; Goulson et al. 2011), while very few studies have been conducted in montane environments (Lozier et al. 2011, 2013). In agricultural landscapes, bumble bee dispersal distances are estimated to be around 2-10 km for males and 1-5 km for new queens (Goulson 2010). A study on two co-occurring species in the Scottish Isles found that one species is capable of dispersing over 30 km, while the other species rarely travels farther than 10 km (Goulson et al. 2011). The common European bumble bee (*B. terrestris*) is capable of dispersing up to 9.9 km (Kraus et al. 2009), while two other European bumble bees (*B. lapidarius* and *B. pascuorum*) are capable of dispersing 3-5 km from their natal site (Lepais et al. 2010).

While these studies provide evidence that bumble bees are capable of dispersing a wide range of distances across simple landscapes, it is important that more studies examine the dispersal abilities of bees in more complex landscapes, such as alpine environments. In response to climate change, species are predicted to shift upward in latitude and elevation into more heterogeneous landscapes. One of the few studies that have examined bumble bees in a more complex landscape, set in the western US, found that populations of two species (*B. occidentalis* and *B. bifarius*) experienced relatively strong genetic drift at high elevations (Lozier et al. 2011). This finding suggests that the montane environments in which these two species are found may lead to genetic isolation in species that would otherwise be weakly differentiated (Lozier et al. 2011). In topographically complex ecosystems, bumble bee dispersal may be limited due to landscape heterogeneity, potentially resulting in greater phylogeographic and genetic structuring (Lozier et al. 2011).

My thesis research addresses questions of spatial genetic structure and potential for interconnectedness among populations of *Bombus balteatus*, a native bumble bee that is

confined to alpine habitats above treeline in the Colorado Rocky Mountains. This system provides an interesting context for examining the interplay of landscape and population connectance due to the heterogeneity of the terrain, which is characterized by a variety of features that could either promote or resist movement of individuals in the region (e.g., deep valleys, high elevation ridges, and variation in vegetation cover).

Mountaintop biogeography and the alpine

Populations in high elevation ecosystems may be considered “island-bound” if the montane habitat patches they occupy occur within a less favorable habitat matrix or are confined by landscape barriers (Brown 1971; Floyd et al. 2005; Lozier et al. 2013). Alpine habitats have been deemed “vertical islands” due to their significant landscape heterogeneity; the steep elevational cline provides gradual changes, creating a mosaic environment above treeline (Martin 2001). Alpine environments have harsh climates that limit what survives there, yet are known to support unique hotspots of biodiversity, making them one of the most complex landscapes in the world (Diaz and Millar 2004). Heterogeneity above treeline is driven by high winds, prolonged snow cover, high aridity, steep terrain, intense ultra-violet radiation, and varying extremes of heat and cold throughout the year (Martin 2001). The alpine is one of the coldest and most relentless biomes, making the biodiversity that does survive there extremely unique. Environmental stochasticity increases with elevation and when combined with a short breeding season and strong seasonality of resources, inhabitants are forced to move to and from very patchy habitats (Martin 2001). To avoid island-effect isolation and loss of genetic diversity, species-specific dispersal abilities are crucial in determining whether an organism survives to another season, or whether it is extirpated from the land above the trees.

Climate change in the Rocky Mountains

The intermountain Western US has experienced significant warming ($>2^{\circ}\text{C}$) over the past few decades at a rate much faster than the rest of the US (Diaz et al. 2014). This warming has occurred at the highest elevations, with another 4°C increase in temperature predicted for the highest mountain ranges by the end of the century (Manino et al. 2007; Diaz et al. 2014). The alpine ecosystem within this region is the only one in the world that exists in all different climatic zones—from the polar region to the equator—and is thus of high ecological concern (Diaz and Millar 2004). Alpine habitats are uniquely sensitive and provide crucial early signals of significant climate-driven changes that are occurring on a global scale (Diaz and Millar 2004). These already fragmented habitats are predicted to go through even further reduction in size under future climate change scenarios, which could compromise inhabitant survival (Manino et al. 2007). The recent warming has caused transcontinental shifts in the timing of species' life cycles and expansion of ranges toward the poles and toward higher elevations (Kerr et al. 2015). As populations track suitable habitat conditions upslope, montane species are predicted to become increasingly isolated, making the species confined to these habitats more at risk to the effects of climate and land-use change in already fragmented habitats (Lozier et al. 2013). Climate change effects will continue to shape alpine habitats and have the potential to cause large-scale local extinctions for species that are already at the edge of their ranges (Manino et al. 2007).

A warming of only a few degrees has major implications for mountain regions; increased temperatures over the past 30 years are already severely reducing snowpack and consequentially shifting snowmelt runoff to earlier in the spring (Diaz et al. 2014). If these trends continue, snowmelt could occur up to a month earlier than has historically occurred in

the Western US (Diaz et al. 2014). A 33 year-long study in Colorado found a significant relationship between snowmelt timing and both peak flowering date and composition of co-flowering plants (Forrest et al. 2010). Climate-mediated changes in co-flowering patterns can reduce the abundance and overlap of flowers that share pollinators and cause competition, which could reduce pollinator visitation to some plant species and could extirpate a particular species from a region (Forrest et al. 2010). Earlier snow melt is also associated with earlier flowering, reductions in flowering periods, and declines in the number of inflorescences on a flower (Forrest et al. 2010). These changes in floral phenology and abundance have the potential to disrupt ecological relationships among plant-pollinator interactions, resulting in altered assemblages of species at the local patch scale and influencing patch selection decisions of pollinators (Forrest et al. 2010).

Any change in the availability of floral resources above treeline can be detrimental to pollinators which depend on them throughout the entire season. There is mounting evidence of non-normality of flowering distributions over the past 35 years; high summer temperatures have caused a bimodal distribution of floral resources, with an overall reduction in total flowers during the middle of the season (Aldridge et al. 2011). This is problematic for pollinators who are dependent upon a unimodal distribution of floral resources, where there is nectar and pollen available throughout the entire season. In an already condensed growing season, bimodality of flowering resources will adversely affect bumble bee colonies by constraining their potential for growth throughout the summer (Williams et al. 2015). Bumble bee peak abundance occurs in the middle of the season, when the queen has produced enough workers to collect resources for colony growth. If there is a longer interval between early and late flowering peaks, then bumble bees may not have enough resources to

provision their nest which would limit the amount of reproductives a queen can produce towards the end of the season (Miller-Rushing and Inouye 2009).

Similar to floral phenology, bumble bee phenology is shifting as a result of earlier snowmelt. Data from museum collections of bumble bees compared to modern inventories show that multiple species are emerging from winter dormancy up to ten days earlier than historic records (Bartomeus et al. 2011). Queen emergence after hibernation in the spring is governed by ground temperature which is controlled by snowmelt; if queens are emerging earlier, this may not coincide with the changes in plant phenology, ultimately causing a disruption in plant-pollinator interactions (Hegland et al. 2009).

Focal species Bombus balteatus

Bombus balteatus was chosen as the focal species for this study because it is the only long-tongued pollinator above treeline in the central Rocky Mountains. It is of particular ecological importance, as there is no other species providing functional redundancy for pollination of specialist long-corolla plants (Miller-Struttman et al. 2015). *B. balteatus* has also experienced significant climate-mediated pressures in the form of loss of floral food resources and increased competition for those resources (Miller-Struttman et al. 2015).

At one site in this study, Pennsylvania Mountain, overall losses of millions of flowers have been observed since the 1970's, explained by increasing summer minimum temperatures over that time period (Miller-Struttman et al. 2015). Concurrently, lowland Colorado bumble bee populations have migrated upward in elevation over the past few decades, similar to patterns observed in the European Alps (Bommarco et al. 2011), leading to a roughly 200% increase in species richness and decreased relative abundance of the two historically dominant alpine bumble bee species, *B. balteatus* and *B. sylvicola* (Miller-

Struttman et al. 2015). It is unclear how these native alpine species will fare under competition floral resources as well as nesting sites, which are a limiting factor for alpine bumble bees (Byron 1980).

Interestingly, *B. balteatus* and *B. sylvicola* at these sites have adapted to the loss of floral resources by adopting more generalized foraging strategies, broadening their diets to incorporate flowers that fall along a greater distribution of corolla tube lengths than their recent ancestors (Miller-Struttman et al. 2015). Concomitantly, both species have also exhibited rapid evolution in the trait that mediates floral visitation, the length of their proboscis (tongue) (Miller-Struttman et al. 2015). Should climate change continue along the current trajectory, shortening may cause a “functional mismatch” between the bees and the long-tubed flowers they once pollinated (Miller-Struttman et al. 2015). Although changes in tongue length are likely to have larger consequences for the flowers (Pyke et al. 2011; Miller-Struttman 2015), the confinement of *B. balteatus* to high elevations (>3,500 m) may make it more susceptible overall to habitat fragmentation and isolation, mediated by food loss and competition. Fortunately, dispersal ability has been found to disproportionately correspond to body size, and *B. balteatus* is at the large end of the distribution for both size and weight, unlike its smaller compatriot *B. sylvicola* (Geib 2010).

Challenges to persistence of *B. balteatus* populations may be part of a larger picture whereby long-tongued bees in general are not faring as well, relative to their short-tongued congeners (Goulson et al. 2005; Colla et al. 2012). Better understanding of how ecologically significant alpine bumble bees utilize their habitat may provide evidence of how other widely distributed species will fare under similar climate-driven conditions.

Habitat suitability

Foraging range

In order to predict how future climate and land-use changes will influence ecologically important species like *B. balteatus*, it is important to know species-specific habitat requirements (e.g., estimates of flight range, how bioclimatic and landscape conditions influence dispersal, and whether any barriers to movement exist). Foraging range is critical to bumble bee ecology as it determines how the landscape is utilized and the area of habitat that can be exploited; bees that can travel further distances to forage and successfully return to their colony may be better at exploiting a patchy habitat in a more heterogenous landscape (Goulson 2010; Geib et al. 2015).

Studies that have examined flight range have found that these ranges vary considerably among bee species; some bees will consistently remain within 500 meters of their nest (*B. pascuorum*, *B. sylvarum*, *B. ruderatus*, and *B. muscorum*), while some forage 1,500 m from their nest (*B. lapidarius*) and others over 2 km (*B. terrestris*) (Goulson 2010). Other studies on *B. terrestris* found that workers would consistently forage between 96-800 meters away from their nest in agricultural landscapes, even when suitable forage was within 50-100 m of a nesting site (Osborne et al. 1999; Wolf and Moritz 2008). This behavior may indicate that bumble bees will not necessarily forage on the closest available patches but may forage further away to minimize intra-colony competition (Dramstad 1996). Foraging distances for several Rocky Mountains species (*B. balteatus*, *B. flavifrons*, *B. bifarius*, and *B. sylvicola*) ranged from only 25-100 m, which indicates that high-elevation bumble bees may have shorter foraging ranges than their lowland counterparts (Geib et al. 2015). This is likely

a result of a shorter blooming season at high elevations, so inhabitants must maximize energy returns more than their lowland congeners (Cameron and Hines 2007; Geib et al. 2015).

Bioclimatic conditions

Many species of bumble bees have a boreal or high mountain distribution which is often disjoint, making them particularly sensitive to land use change and climate variation (Manino et al. 2007). Climatic factors greatly influence high elevation species and may limit their geographic distribution (Lozier et al. 2011; Pyke et al. 2011; Kudo 2013; Williams et al. 2015). The stark contrast between summer and winter climates can greatly influence these bees, which require suitable year-round temperatures and sufficient yearly precipitation to provide both snowpack to insulate hibernation sites and rain for floral resources (Lozier et al. 2013). Maximum extremes of temperature and solar radiation may cause water deficits and reduce nectar and pollen production (Hijmans et al. 2005; Williams et al. 2015). High precipitation may reduce foraging opportunities; heavy rainfall can impede a bees ability to fly and bees avoid pollen when it is wet because it can become too sticky (Pyke et al. 2011), while extremely low precipitation may decrease floral abundance and reduce food production (Hijmans et al. 2005).

Barriers to dispersal and gene flow

Strong genetic structuring occurs when populations are separated by such appreciable barriers, while little genetic structuring occurs when no substantial barriers between populations exist (Goulson 2010). Potential barriers to bumble bee dispersal include geographic distance (Rasmont et al. 1983; Ellis et al. 2006), bodies of water (Widmer et al. 1998; Hingston 2006; Goulson 2010), impervious surfaces (Jha and Kremen 2013), floral resources (Persson and Smith 2013), and mountain ranges (Pirounakis et al. 1998; Widmer

and Schmid-Hempel 1999). Some studies have found that sea barriers between 3-10 km wide are sufficient to restrict gene flow between populations (Darvill et al. 2006; Hingston 2006; Darvill 2007), while other studies have found that bees are capable of traversing bodies of water that are 30 km wide (Darvill 2007; Goulson 2010). Island populations have exhibited reductions in heterozygosity and significant differentiation compared to mainland populations, indicating that water may provide resistance to dispersal and may make populations at risk for isolation (Bourke and Hammond 2002; Shao et al. 2004).

Contemporary land-use changes associated with commercial, industrial, and transportation related impervious cover have been found to limit dispersal in populations near urban and suburban areas (Jha and Kremen 2013). Simple landscapes with limited floral resources and nesting habitats have been found to limit bumble bee abundance and species richness compared to complex landscapes with high availability of resources throughout the season (Persson and Smith 2013). Mountain ranges may function as barriers to dispersal for some species that are separated by 9-32 kilometers (Rasmont 1993; Pirounakis et al. 1998; Widmer and Schmid-Hempel 1999) while other populations show very little population structuring (Estoup et al. 1996).

Landscape heterogeneity and metapopulation dynamics

Landscape heterogeneity influences spatial distribution and dispersal ability influences how species are able to move within and between suitable patches of habitat (Baguette and Dyck 2007). Landscape connectivity shapes individual movements and influences the degree to which the landscape facilitates or impedes movements of individuals between resources patches (Baguette and Dyck 2007). Heterogeneity may cause species to aggregate in areas where there are abundant food resources and shelter and yet is equally

likely to cause species to move between habitat patches, incurring risks and possibly even death (Shen et al. 2009). Spatial variation thus influences how animals are distributed, how they perceive and respond to their environment, and ultimately why and when they disperse across the landscape (Kie et al. 2002).

The goal of many biodiversity studies is to understand the relationship between the distribution of genetic diversity and environmental heterogeneity. Variation in dispersal ability and propensity to disperse influences metapopulation dynamics as it influences a populations' ability to persist in fragmented habitat patches (Hawkes 2009; Goulson et al. 2011). The ability to navigate, orient, and disperse over long distances and to adopt straighter and faster movements, especially where suitable habitat is patchy, can increase metapopulation viability (Baguette and Dyck 2007). Movement behavior and species-specific dispersal abilities can indicate how metapopulations will fare in unpredictable landscapes and changing environments.

Landscape features such as habitat quality and patch size are known to affect pollinator composition by influencing dispersal, foraging, and nesting abilities and landscape connectivity has been found to significantly impact pollinator communities by decreasing phylogenetic diversity (Adderly and Vamosi 2015). Source-sink dynamics and gene flow are likely to increase likelihood for dispersal, which necessitates an understanding of the metapopulation dynamics and gene flow among populations (Hadley and Betts 2012). Within a functioning metapopulation, dispersal ensures that local extinctions are followed by recolonizations; however, if habitat heterogeneity and fragmentation lead to larger distances between patches or isolation of patches, then suitable patches of habitat may remain unoccupied (Darvill et al. 2009). Metapopulation theory predicts that extant populations with

greater interconnection via dispersal and gene flow may be more likely to withstand environmental challenges and should therefore exhibit greater likelihood of persistence (Hanski and Gilpin 1991).

Predictions and implications

The aim of my research was to assess the importance of the landscape in determining the genetic structure of *B. balteatus* populations in the central Rocky Mountains using microsatellite markers and resistance models. Genetic structure (measured with microsatellite markers) can be used to indirectly measure dispersal and gene flow, which are directly related to how well individuals can fulfill important biological processes (foraging, mating, migration) and persist in their environment (Zeller et al. 2012). Landscapes may provide resistance to movement, depending on the willingness of an individual to disperse across a particular environment and the costs associated with movement (Zeller et al. 2012). If *B. balteatus* is limited in dispersal between high alpine habitats due to various resisting landscape factors or barriers to gene flow, then I expect to see low genetic diversity and heterozygosity within populations and high genetic structuring among populations.

I hypothesize that *B. balteatus* populations are functioning as a metapopulation by occupying discrete habitat patches within a larger matrix of unsuitable habitat. If this is true, I expect to see patterns of isolation by distance, where populations that are closer to one another are more genetically similar than those that are farther apart. I also expect to see patterns of isolation by resistance, where populations that are connected by favorable habitat (flowering ridgelines with high sun, low wind, and moderate precipitation) will be more genetically similar than those that are separated by unfavorable habitat (low elevation forested valleys with low sun, high wind, and extremes of precipitation). When populations

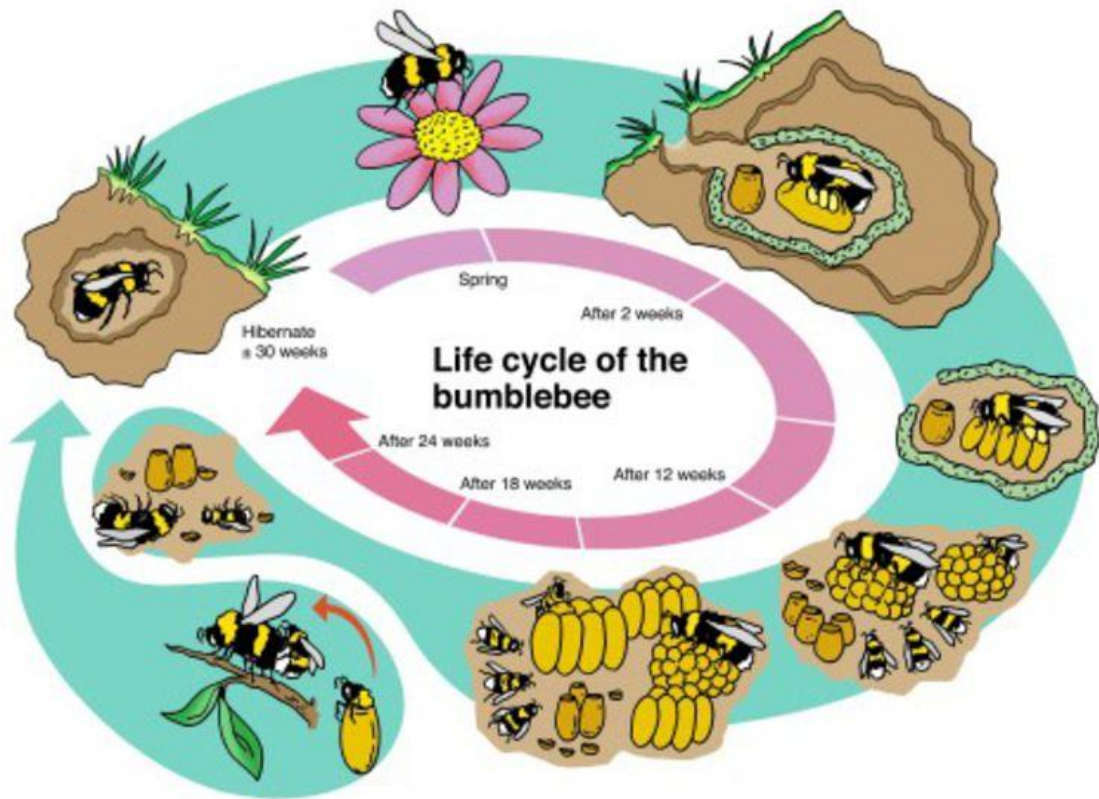
are separated by a homogenous landscape, genetic differentiation will most likely have a significant positive relationship with physical distance. However, if populations are separated by complex heterogeneous landscapes, geographic distance alone might not predict genetic differentiation. Therefore, I predict that incorporating various environmental and landscape variables into models, other than modeling geographic distance alone, will better predict dispersal and gene flow for *B. balteatus*.

Measuring *B. balteatus* dispersal and gene flow indirectly via genetic structuring may have unique implications for how other bumble bees disperse across a heterogeneous landscape. Estimating the dispersal abilities of bumble bees is critical for understanding how native bees will fare in the face of environmental challenges. The ability to predict pathways of dispersal among populations and to identify environmental factors that shape these paths have clear implications for conservation; we may need to facilitate dispersal pathways and aid in the spatial arrangement of suitable habitat to prevent isolation and potential extinction (Lozier et al. 2013).

Figure Legends

Figure 1 The life cycle of a bumble bee (Natupol.com)

Figure 1



Chapter 2

GENETIC STRUCTURE AND GENE FLOW BARRIERS AMONG POPULATIONS OF AN ALPINE BUMBLE BEE (*BOMBUS BALTEATUS*) IN THE CENTRAL ROCKY MOUNTAINS

INTRODUCTION

Pollinators are responsible for facilitating nearly 90% of all flowering plant species reproduction and for increasing the quantity and quality of over 60% of the worlds crops (Jha and Kremen 2013). Bees, particularly bumble bees, are one of the most important and effective pollinators and are considered keystone species within plant-pollinator communities because they pollinate both abundant and rare plant species (Jha and Kremen 2013). Bumble bees have faced significant declines in relative abundance and geographic range over the past few decades (Cameron et al. 2010), largely attributed to habitat fragmentation and loss, agricultural intensification, pathogens and diseases, competition with non-native species, and increased use of pesticides and insecticides (Cameron et al. 2010; Darvill et al. 2006; Dreier et al. 2014; Hadley and Betts 2012).

Bumble bees are particularly susceptible to decline due to their low effective population sizes, low genetic variation from haplo-diploidy, and their monoandrous mating system (Darvill et al. 2006). Although colonies can contain upwards of 200 workers, only one reproductive queen is responsible for producing all the offspring, meaning that even apparently abundant populations may actually have limited genetic diversity and may be more vulnerable to stochastic effects (Dreier et al. 2014). Dispersal of individuals across

landscapes is essential for gene flow, maintaining adaptive genetic variation, and preventing inbreeding within the population (Jha and Kremen 2013). Patterns of dispersal and gene flow are key determinants of a species' ability to respond to population pressures (Jha and Kremen 2013).

This study examines population structure and evidence and mechanisms for gene flow among populations of *Bombus balteatus*, a native bumble bee species that occupies habitats above treeline in the central Rocky Mountains. *B. balteatus* populations in these habitats have experienced significant challenges that make understanding their ability to disperse, exchange genes, and respond to population pressures critically important. Parallel to trends seen worldwide (Bommarco et al. 2011), lowland bumble bee species are moving upward in elevation, creating competition for floral resources and nesting sites, which are themselves limited (Miller-Struttmann et al. 2015). Few studies have examined bumble bee gene flow processes (Dreier et al. 2014) or dispersal at local spatial scales across heterogeneous landscapes (Jha and Kremen 2013) with the exception of agricultural or manipulated landscapes (Drier et al. 2014; Goverde et al. 2002; Carvell et al. 2011; but see Goulson et al. 2011; Lozier et al. 2013). The highly heterogeneous mountainous landscape provides a more complex context in which to examine these concepts. In topographically complex ecosystems, bumble bee dispersal may be limited due to landscape heterogeneity, potentially resulting in greater phylogeographic and genetic structuring (Lozier et al. 2011).

The specific aims of this study were to 1) determine the genetic structure of *B. balteatus* populations in the central Rocky Mountains using microsatellite markers and 2) to assess the importance of the landscape in contributing to the genetic structure of *B. balteatus* using habitat suitability and connectivity models. Genetic structure (measured with

microsatellite markers) can be used to indirectly measure dispersal and gene flow, which are directly related to how well individuals can fulfill important biological processes (foraging, mating, migration) and persist in their environment (Zeller et al. 2012). Resistance represents the willingness of an individual to disperse across a particular environment and the costs associated with movement (Zeller et al. 2012). If *B. balteatus* is limited in dispersal between high alpine habitats due to various resisting landscape factors or barriers to gene flow, then I expect to see low genetic diversity and heterozygosity within populations and high genetic structuring between populations.

I hypothesize that *B. balteatus* populations are functioning as a metapopulation by occupying discrete habitat patches within a larger matrix of unsuitable habitat. If this is true, I expect to see patterns of Isolation by Distance, where populations that are closer to one another are more genetically similar than those that are farther apart. I also expect to see patterns of Isolation by Resistance, where populations that are connected by favorable habitat will be more genetically similar than those that are separated by unfavorable habitat. When populations are separated by a homogenous landscape, genetic differentiation will most likely have a significant positive relationship with physical distance. However, if populations are separated by a complex heterogeneous landscape, geographic distance alone might not predict genetic differentiation. Therefore, I predict that incorporating various environmental and landscape variables into models, other than modeling geographic distance alone, will better predict dispersal and gene flow for *B. balteatus*.

METHODS

Study sites

Samples for this study were collected at 9 different locations above tree line in Clear Creek, Park, Summit, Chaffee, and Lake counties in Colorado, USA (Fig. 1). I selected sites for data collection based on variation in geographic distance among sites and in potential dispersal pathways that could either favor or limit gene flow. Sites also varied in landscape characteristics such as elevation, precipitation, and land use. The sites span an area of ~8,000 km² in the central Rocky Mountains.

Study system

Bombus balteatus was chosen as the focal species for this study because it is one of two native bumble bees in the alpine habitats that comprise the focus of this study. It is of particular ecological importance as the only long-tongued pollinator above treeline, where no other species provides functional redundancy for pollination of specialist long-corolla plants (Miller-Struttmann et al. 2015). Queens of *B. balteatus* emerge around mid-June during snowmelt and may disperse away from their overwintering habitat in search of a nesting site. Workers emerge in early July, foraging throughout the season to provision resources for the nest until emergence of new queens and drones at the end of the season (late-July to mid-August). This time comprises a second round of possible dispersal of individuals and their genes among populations as new queens and drones move away from nest sites to avoid inbreeding (Goulson 2010). Once new queens have mated, they disperse in search of overwintering sites, which comprises the third and final round of possible dispersal.

B. balteatus is confined to high elevations (>3,500 m) and may therefore be more susceptible to habitat fragmentation, population genetic structuring, and even isolation (Lozier et al. 2013). However, dispersal ability has been found to disproportionately correspond to body size, and *B. balteatus* is a relatively large species, which may influence its ability to disperse (Greenleaf et al. 2007). An influx of novel alleles into a *B. balteatus* population was observed at one study site (Pennsylvania Mountain) following drought-mediated decimation of the population in 2012 (Rimmer 2015). This influx of new alleles indicates connectedness to other populations and may ultimately indicate that populations of *B. balteatus* are capable of withstanding stochastic environmental events.

Field collection

I systematically collected specimens for this study at nine sites in July and August of 2017. I lethally sampled a minimum of 25 *B. balteatus* workers from each site to ensure proper species identification and to ensure that I would have enough samples from each site ($n \geq 10$) for genetic analyses. Lethal sampling of foraging workers has no detrimental effects to a colony or brood rearing and does not affect bee communities in terms of abundance, richness, evenness, or functional group composition (Gezon et al. 2015). A single colony can produce 50-200 workers, and anywhere from 18-78 colonies are present within a 0.01 km² area so it is rare to sample more than 1-2 workers from a single colony (Geib et al. 2015). I sampled populations during full bloom and peak worker abundance (July 19th- August 5th) to minimize negative effects of worker removal on brood rearing (Pyke et al. 2011).

Collections occurred at one site per day and the sites were sampled in a random order. Some sites were visited twice to obtain the minimum number of samples (Democrat, Boreas, Horseshoe, and Niwot Ridge). I collected specimens at multiple locations across the

elevational gradient within each site to minimize the probability of sampling individuals from the same colony (Goulson et al. 2011). I began sampling each site at the highest elevation above tree line (~ 4,200 meters) with suitable habitat (i.e., grassy areas with floral resources) and then sampled areas of suitable habitat every 100-200 m in descending elevation until I reached tree line (~ 3,500 m). In previous studies of other bumble bee species, this distance between sites has been found sufficient to avoid sampling of sisters (Darvill et al. 2010).

At each elevation, I recorded GPS coordinates, approximate temperature and cloud cover, and general weather notes. Collections occurred for approximately 1 hour at each elevation. I used a mesh aerial insect net (30 cm diameter, Bioquip) to net any observed bumble bees along an approximately 50 meter transect (~.01 km²) at each elevation. Most bumble bees were caught foraging on flowers and the flower was identified to genus and recorded for each sample (Table A1). All bees were directly placed into 20 mL plastic vials and were then cooled to torpor on ice (~10-15 minutes, until immobilized by the cold) for easier handling and identification. Upon completion of the survey period, queens and non-focal species were preliminarily identified and released on site at each respective elevation. Identifications were made in accordance with Koch et al. (2012) and Byron (1980). Specimens for analysis were stored in molecular grade ethanol and transported to Appalachian State University in a cooler on dry ice and were kept in a -20°C freezer.

Molecular methods

DNA extraction

I extracted DNA from all specimens in the Fall of 2017 using a PureLink® Genomic DNA Mini Kit (Invitrogen). The protocol was modified from mammalian tissues and mouse/rat tail guidelines described in the kit manual. Approximately 0.50 grams of

abdominal tissue was used to prepare the lysate, which was digested with Proteinase K and digestion buffer. The lysate was mixed with ethanol and binding buffer that bound the DNA to a spin column with a silica-based membrane. Impurities were removed through washing with two wash buffers, and DNA was eluted in a low salt elution buffer. Sample concentration and purity content was analyzed using a Nanodrop® spectrophotometer and gel electrophoresis ensured DNA was extracted from each sample.

Amplification of microsatellites

All samples were genotyped with the following ten DNA microsatellite markers: B10, B96, B119, B124, BTERN01, BTERN02, BL11, BL13, BT10, and BT28 (sensu Geib et al. 2015). Multiplex polymerase chain reactions (PCR) were carried out on samples and run for combinations of the loci B124(FAM)-BL11(PET)-BL13(PET)-BTERN01(VIC)-BT10(NED) and B96(PET)-B119(VIC)-BTERN02(NED)-B10(FAM)-BT28(VIC) (fluorescent markers indicated in parentheses). PCR reactions were 10 µl in volume and consisted of 1 µl of template DNA, approximately 340 µl of UV-treated and reverse osmosis water, 220 µl of Promega 5X Buffer, 61.6 µl of MgCl₂, 66 µl of dNTP's, approximately 270 µl of combined reverse and forward primers, 22 µl of Bovine Serum, and 8.8 µl of Promega Flexi GoTaq® polymerase. Samples were denatured at 95°C for 7 minutes, followed by thirty 90-second cycles consisting of a denaturing step at 95°C for 30 seconds, an annealing step at 54°C for 30 seconds, and an extension step at 72°C for a further 30 seconds. This was then followed by a final extension step at 72°C for 1 hour, based on optimization trials (sensu Geib et al. 2015). PCR products were visualized on a capillary DNA sequencer at the University of Georgia Genomics and Bioinformatics Lab (Athens, GA) with a 1:80 dilution before the run and using a GeneScan LIZ 500 internal size standard (Applied Biosystems).

Genetic data analysis

Genotyping microsatellites

Raw allele sizes were scored manually and binned into discrete classes using GeneMapper® 4.0 (Applied Biosystems, 2005). Samples for which amplification was not successful, or scoring was uncertain, were re-run and re-extraction of DNA was carried out if necessary. Any individuals that failed to amplify after repeated attempts were excluded from the final dataset. The primers BTERN02 and B119 were omitted from further analyses because the former was monomorphic and the latter was extremely poor in quality for almost all samples.

Identification and removal of sibling workers

Colony v. 2.0 (Jones and Wang 2009) was used to identify and remove siblings for subsequent analyses, ensuring that genetic differentiation was not confounded by pseudo-replication and family structure. This program uses maximum likelihood methods to assign sibship or parent-offspring relationships and has been found to be one of the most reliable methods for assigning sibship in bumble bees (Lepais et al. 2010; Goulson et al. 2011). Full sisters share 75% of genes by descent, so assigning sibship in haplodiploid species is very reliable (Goulson et al. 2011).

I assumed “male polygamy” and “female monogamy”, as *B. balteatus* does not belong to the subgenus *pyrobombus*, which is known for polyandry (Estoup et al. 1996). However, all combinations of mating systems were tested to determine the effect of mating system on family reconstruction. I also assumed lack of inbreeding, because no evidence currently has been observed for such within these populations, and selecting the inbreeding model for the data had little to no improvement for the estimation of sibship. “Without clone”

was chosen because all offspring genotypes were assumed to come from distinctive individuals who were not clone mates.

The genetic markers were specified as codominant, allelic dropout rate was set to 0.0000, and genotyping error was set to 0.0075. There are few strategies for effectively quantifying genotyping error, yet most studies report an error rate between 0.5 and 1%, so 0.75% was selected for the error rate for all markers (Pompanon et al. 2005). Population allele frequencies were unknown and the total number of offspring was 392, all of which were selected as candidate female genotypes because no males were included in this study. Paternal and maternal sibship, paternity, and maternity were all unknown and excluded paternity, maternity, paternal siblings and maternal siblings were all set to 0. The probability of a mother being included in the samples was 0.01, as all identified queens were released on site during collection. All individuals inferred by Colony in the full-sib dyad were removed that had a probability of such a dyad greater than 0.50.

Population genetics testing

I assumed that sampling localities were equivalent to populations for all population genetics testing. The genotype data were tested for deviations from Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium (LD) using the Markov chain method (dememorization = 1000, batches = 100, iterations per batch = 1000) as implemented in Genepop v 4.1.2 (Raymond and Rousset 1995). Heterozygote excess and deficiency were also tested for each locus and population as well as across all loci and populations using the Score U test as implemented in Genepop. Log-likelihood ratio tests and probability tests for linkage disequilibrium were tested for each locus pair and population in Genepop.

Population differentiation estimates

I estimated total allele frequencies, average alleles per locus, and the expected and observed numbers of homozygotes and heterozygotes for each population and locus in Genepop. Allelic richness (after correction for population size) and unbiased estimates of heterozygosity were estimated for each locus and population in Fstat v 2.9.3 (Goudet 2002). Genetic differentiation between populations were estimated and tested for significance with F_{ST} (Wright 1943), G_{ST} (Nei 1972), and G'_{ST} (Meirmans and Hedrick 2011) in Fstat. Pairwise F_{ST} were transformed to $F_{ST}/(1-F_{ST})$ with Genepop (Weir and Cockerham 1984). I estimated the inbreeding coefficient (F_{IS}) for each locus and population and tested for significance using an AMOVA with 1000 permutations as implemented in Fstat.

Genetic clustering

Genetic population structure was calculated using Bayesian genetic clustering in Structure v 2.3.4 (Pritchard et al. 2000). The Admixture and Correlated Allele Frequency models were used and the software was run with the number of clusters (K) varying from 1 to 9, with ten runs for each K value using 10,000 burn in periods and 50,000 Markov Chain Monte Carlo (MCMC) repetitions (Falush et al. 2003). The web-based software program Structure Harvester v 0.6.94 (Earl and VonHoldt 2012) was used to visualize the results and determine the number of populations using both the mean of estimated Ln probability of data ($\text{LnP}(D)$) and Delta K (Evanno et al. 2005) methods. An additional long run using the best K value for both methods were ran with 50,000 burn in periods and 100,000 MCMC repetitions to obtain the final structure results.

Estimating spatial patterns of genetic structure

Estimating isolation by distance

I assessed the correlation between geographical distance (and its decimal logarithm) and genetic differentiation (expressed as $F_{ST}/(1-F_{ST})$) using linear regression and tested for significance using a Mantel test (Legendre and Legendre 1998) implemented in the R package 'ade4' (Thioulouse et al. 2018).

Environmental niche modeling

I obtained spatially explicit environmental variables for contemporary conditions from the WorldClim V1.4 (Hijmans et al. 2005). Nineteen bioclimatic variables and monthly (June-August) averages of seven variables were downloaded at 30 arc-second ($\sim 1 \text{ km}^2$) resolution. I downloaded the digital elevation model (DEM) for the study site area from the Colorado Geological Survey (Homer et al. 2015) and land, tree canopy, and impervious cover estimates for the conterminous United States from the National Land Cover Database of circa 2011 Landsat satellite data (Xian G et al. 2011). All bioclimatic and landscape variables were clipped to the study area extent using ArcMap 10.3.1 (ESRI, Redmond CA). Each layer was projected into the WGS 1984 geographic coordinate system and clipped to the same cell size (0.0083, 0.0083), number of columns and rows (249, 234), and spatial extent (Top: 40.475, Left: -107.1, Right: -105.025, Bottom: 38.525). Each layer was then converted from raster to ASCII format using the ArcMap toolbox.

I reduced autocorrelation of environmental data by removing highly positively correlated variables in order to avoid any limitation of inference of the contribution of each variable (Alvarado-Serrano and Knowles 2014). I used the R packages 'raster,' 'dismo' and 'usdm' to remove correlated variables; the 'raster' package manipulates geographic and spatial data in raster format, the 'dismo' package implements species distribution model methods, and the 'usdm' package assesses different sources of uncertainties on performance

of species distribution models (Hijmans et al. 2017; Naimi 2017). I set the correlation threshold to $\theta \geq 0.70$ and one variable in each pair of correlated variables was retained. I tested for collinearity within the 19 bioclimatic variables, the 19 bioclimatic variables and landscape variables (land-use, elevation, imperviousness, and tree canopy cover), and then within the 21 monthly variables (July-August monthly averages for 7 climatic variables).

I downloaded spatially referenced natural history occurrence records for *B. balteatus* from the Global Biodiversity Information Facility (GBIF.org). I only used records that occurred in the United States from contemporary collections or observations from 1970 to the present (to correspond with available landscape and environmental data). I also compiled occurrence records from data collected at Pennsylvania Mountain, Colorado in 2015 (Geib et al. 2015) and from Niwot Ridge and Mt. Evans, Colorado in 2012-2014 (Miller-Struttmann et al. 2015). Specimens that fell outside of the study extent were excluded and a total of 741 records remained.

MaxEnt: maximum entropy modeling

To quantify landscape heterogeneity and habitat suitability, I generated environmental niche models (ENM) using the principle of maximum entropy as implemented in the program MaxEnt v 3.3.3 (Elith et al. 2010; Phillips et al. 2009). MaxEnt uses presence-only locality data and background points randomly sampled from the study area to estimate the species distribution that is closest to uniform (i.e., maximizes entropy), given information on the environmental conditions of the study area. I ran univariate models to determine the independent effects of each bioclimatic and landscape variable on species distribution. I then ran multi-variate models with various combinations of covariates to determine the model that best estimated environmental suitability for *B. balteatus*. I developed 3 multi-variate ENM's

that modeled the effects of all bioclimatic variables, all climate variables for June-August, and all landscape variables on *B. balteatus* distribution. I developed 5 ENM's that modeled the effects of these same variables (and combinations of them), once correlated variables were removed. Finally, I developed two ENM's that were based on variables that I hypothesized a priori to affect *B. balteatus* gene flow; these variables capture bioclimatic trends that are likely to be relevant to bumble bees (suitable year-round temperatures and sufficient yearly precipitation to provide rain for floral resources and snowpack for hibernation) (Aldridge et al. 2011; Lozier et al. 2013).

The 25 percentile training presence (i.e., the value above which the model classifies correctly 75% of the training locations) was selected as the threshold value for defining *B. balteatus* presences. I used jackknife sensitivity analysis to estimate the contribution that each variable gave to the geographic distribution models (percent contribution) which is modeled in MaxEnt first by excluding each variable in turn and creating a model with the remaining variables and second by individually adding each environmental variable to the model to detect which variable has the most information that is not featured in the other variables. All models were run to generate a logistic output for 5000 iterations and averaged over 10 sub-sampled replicates. All other settings remained default unless otherwise noted (Phillips et al. 2009).

Accounting for sampling bias

Sampling biases (e.g., sampling easily accessible areas near roads or towns) can artificially increase spatial auto-correlation of localities, causing the model to overfit to environmental biases that correspond to these influences in geographic space. If sampling is biased, it is difficult to distinguish whether species are observed in particular environments

because those locations are preferable, or because they received a larger search effort (Merow et al. 2013). Sampling bias can limit the model's ability to accurately predict species distributions or environmental niche and can result in over or underfitting of the model and/or inflated model performance. When sampling bias is accounted for, the null hypothesis states that individuals have only been observed in particular locations because those were the places that were sampled (i.e., individuals are uniformly distributed in geographic space) (Merow et al. 2013).

One method to account for sampling bias is to limit where background points are selected from by only allowing MaxEnt to select from counties where there are known sample locations, which limits the background points to areas that were surveyed and provides MaxEnt with a background file that has the same bias as the presence locations (Young et al. 2011). I first created a shapefile of the location points in ArcMap v 10.3.1 and then downloaded a map of US counties (ESRI, 2018) and selected only the counties with recorded *B. balteatus* presences within them. I used Map Algebra in ArcMap to convert this new raster to have a value of 1 in the selected counties and a value of "No Data" everywhere else. I then clipped all the environmental layers to this new raster layer. The county raster file was input into MaxEnt as a bias file so that background points were only selected from the counties with known occurrence records.

Model validation

Model accuracy was estimated by the area under the receiver-operating curve (AUC), which is a rank-based metric for model fit and can be interpreted as the probability that a randomly chosen presence location is ranked higher than a randomly chosen background

point (Elith et al. 2010; Merow et al. 2013). Models with an AUC above 0.75 are considered to have high predictive accuracy and discrimination performance (Phillips et al. 2009).

Modeling dispersal pathways and resistance to dispersal

To test how environmental and landscape factors might influence dispersal, I used Circuitscape v 4.0 to model dispersal pathways between all sites and to create resistance surfaces (McRae 2006). Contrary to least cost resistance methods which assume that individuals disperse according to previous knowledge of the landscape, Circuitscape considers the effects of all possible pathways for dispersal across a landscape simultaneously and expresses the model predictions in terms of random walk probabilities (Spear et al. 2010). Landscape connectivity thus increases according to the number of connected pathways between each habitat patch.

Circuitscape borrows algorithms from electrical circuit theory to model the landscape matrix between populations as an electronic circuit; the ease with which individuals (or genes) disperse between two populations is modelled by the way electric current flows between two points in a circuit (McRae 2006). Each cell in the raster map representing the landscape and a parameter of interest (e.g., elevation, precipitation, land-use) is modelled by an electric resistance; low resistance values are assigned to landscape features that are most permeable to movement (or best promote dispersal and gene flow) and high resistance values are assigned to features that are essentially barriers to movement (or inhibit dispersal and gene flow) (McRae 2006). Circuitscape uses this resistance data to calculate effective pairwise resistances between sites and create maps of current flow and voltage across a landscape, which are termed resistance surfaces (McRae 2006). Locations on these maps with high values or narrow widths may be features or regions in the landscape that are

important for habitat connectivity and dispersal pathways for a particular species in the study area.

Estimating Isolation by Resistance

I tested for the presence of a pattern of isolation by resistance (IBR) by combining the MaxEnt models of environmental niche (relative habitat suitability) with the circuit theory approach implemented in Circuitscape (habitat connectivity). The univariate and multivariate models were first input into MaxEnt to model environmental niche and habitat suitability and then each logistic output raster was input into Circuitscape as the conductance layer, where areas of high predicted suitability values specify greater conductance and connectivity, and thus the potential for greater dispersal and gene flow. Circuitscape was run in pairwise mode with the four-neighbor cell connection scheme for all models. The resulting pairwise resistance matrices were then correlated with the previously described genetic differentiation matrix ($F_{ST}/1-F_{ST}$) to test for isolation by resistance (IBR) using linear regression as well as a Mantel test (Legendre and Legendre, 1998) implemented in the R package “ade4” (Thioulouse et al. 2018).

RESULTS

Field collection and genetic data analysis

A total of 446 *B. balteatus* workers were sampled across 9 mountain sites, with collections ranging in elevation from 3473 meters to 4012 meters (Table 1; Table A2). The number of individuals caught per site ranged from 16 to 96, and the mean individuals caught per site was 50 ± 20.89 S.E.

A total of 404 individuals were genotyped for eight microsatellite loci. Out of these individuals, 12 failed to amplify for more than 4 loci and were excluded from further analyses. 358 unique family groups (colonies) were detected with the mean number of colonies per site being 37.8 ± 5.10 S.E. A total of 47 sister pairs were detected under the assumption of male polygyny and female monoandry, the most likely scenario for *B. balteatus*. Changing the assumed mating system to male and female polygamy produced 68 pairs, 37 of which were unanimous regardless of mating system. All pairs had ≥ 0.5 probability of sibship. Following the removal of sibling workers as identified under the female monoandrous system, the remaining analyses were conducted with a total of 358 individuals.

The total number of alleles detected per polymorphic locus ranged from 4 (locus BT28) to 21 (locus B96) and the average number of alleles per locus was 15 (Table 2).

Population genetics testing

Hardy-Weinberg (HW) expectations were rejected in 32 out of 72 cases (Table A3). The significant cases were not clustered by locus or population, however loci BT10 and B10 had the highest number of populations in departure of HW and the Silverheels and Evans populations had the highest number of loci in departure of HW. Heterozygote deficiency was significant in 37 out of 72 cases, while heterozygote excess was not significant in any cases. The significant values were not clustered by populations or locus, rather all populations and loci exhibited some significant deficiency in heterozygotes.

Log-likelihood ratio tests detected a highly significant linkage disequilibrium (LD) for 3 out of 28 locus pairs: B124-BTERN01, B124-B10, and BT10-B10 (Table A4). Probability tests detected LD for the same three pairs of loci, as well as an additional pair:

BT10-B96 (Table A4). LD was found in 16 of 252 cases among the analyzed loci and populations when tested with the log-likelihood ratio statistic and in 15 out of 252 cases when tested with the probability test (Tables A5, A6). No common pair of loci deviated from equilibrium in all populations.

Population differentiation estimates

The mean number of alleles per locus per population (observed allelic diversity) ranged from 10.7 ± 3.9 (Elbert population) to 14.9 ± 5.5 (Democrat population) (Table A7). After correcting for sample size ($n=15$), overall allelic richness was 9.22 (Table 3). The Niwot population had the lowest allelic diversity (8.39), while the Elbert population had the highest (9.88). The overall level of expected heterozygosity was moderately high across populations (overall H_E : 0.809). The Niwot population had the lowest average expected heterozygosity across all loci (H_E : 0.784), while the Elbert population had the highest (H_E : 0.8303). The overall level of observed heterozygosity was lower than expected (overall H_O : 0.723). The Silverheels population had the lowest observed heterozygosity (H_O : 0.647), while the Quail population had the highest (H_O : 0.803).

The inbreeding coefficient (F_{IS}) varied among populations, with overall $F_{IS}= 0.107$. (Table 3). F_{IS} estimates for each locus and population were positive in 56 out of 72 cases (Table A8). Genetic variation was relatively low, with overall $F_{ST}=0.019$. Pairwise comparisons of F_{ST} between populations ranged from -0.0002 to 0.0434 and were significant in 28 out of 36 comparisons ($0.00139 < P < 0.0389$) (Table 4). Democrat and Silverheels populations were the most genetically dissimilar (pairwise $F_{ST} = 0.0434$), followed by Democrat and Niwot ($F_{ST} = 0.0418$) and Democrat and Quail ($F_{ST} = 0.0392$). Boreas and

Elbert populations were the most genetically similar ($F_{ST} = -0.0002$), followed by Niwot and Silverheels ($F_{ST} = 0.0001$) and Democrat and Evans ($F_{ST} = 0.0001$).

Per locus estimates of expected heterozygosity (H_E) ranged from 0.487 (locus BT28) to 0.902 (locus B96) (overall $H_E = 0.809$) (Table 5). Observed heterozygosity (H_O) ranged from 0.443 (locus BT28) to 0.881 (locus B96), with overall $H_O = 0.723$. Total gene diversity (H_T) ranged from 0.489 (locus BT28) to 0.908 (locus B96), with overall $H_T = 0.822$. Per locus F_{IS} estimates ranged from 0.029 (locus B96) to 0.152 (locus BT10). F_{ST} estimates ranged from 0.003 (BTERN01) to 0.094 (locus B124). Multi-allelic estimates of genetic differentiation (G_{ST}) ranged from 0.001 (locus BL11) to 0.071 (locus B124), with overall $G_{ST} = 0.016$. Estimates of G'_{ST} ranged from 0.001 (locus BL11) to 0.079 (locus B124), with overall $G'_{ST} = 0.018$.

Genetic clustering

Among the ten repeated analyses for each of the possible number of genetic groups ($K = 1-9$), the most likely number of populations was $K=6$ using LnP(D) estimates and $K=3$ using delta K estimates (Fig. 2). The bar charts for both $K = 6$ and $K = 3$ show that the Democrat, Boreas, Evans, and Elbert populations form a distinct cluster (Fig. 3a: predominantly yellow and turquoise segments; Fig. 3b: predominantly green segments), while the Horseshoe, Penn, Quail, Niwot, and Silverheels populations form a separate cluster (Fig. 3a: predominantly hot pink segments; Fig. 3b: predominantly dark blue segments). Although K estimates differ between methods, they both show the same general pattern of clustering, so the LnP(D) method will be used for further discussion of results, as it shows more individual differences.

The dark blue genetic cluster is only represented by a few individuals that are scattered among different populations (Fig. 4: Evans, Boreas, Democrat, and Penn). The red genetic cluster is minimally represented across all populations, however it does appear more frequently in some populations (Fig. 4: Niwot, Silverheels, Penn, and Horseshoe). The green genetic cluster is also represented by only a few individuals in most populations and is most represented in the southernmost population (Quail). The neighborhood joining tree plot reveals this cluster as the most distantly related genetic cluster (Fig. 5).

Globally, the hot pink, yellow, and turquoise genetic clusters are most represented across all populations and help distinguish the clusters the most. The yellow and turquoise genetic clusters are most predominant in the upper central sites (Democrat, Boreas, and Evans) while the hot pink genetic cluster is most predominant in the lower central sites (Penn, Silverheels, Horseshoe). There are two exceptions to this general pattern, however, as the Niwot population appears more genetically similar to these latter populations despite being the farthest north in the study area. The Elbert population appears to be more genetically similar to the upper central sites, despite being one of the southernmost sites.

Estimating spatial patterns of genetic structure

Estimating Isolation by Distance

Distances between populations ranged from 8.33 km (Democrat and Penn) to 133.87 km (Niwot and Quail) (Table 6). There was no significant pattern of isolation by distance (IBD) when correlating pairwise Euclidean distance with pairwise F_{ST} between populations (Table 6; Fig. 6) or pairwise log of Euclidean distance with pairwise F_{ST} between populations (Table 7, Fig. 7). The observed Mantel statistics were -0.041 ($P= 0.7547$, $N= 9999$ replications) and 0.005 ($P= 0.497$, $N= 9999$ replications) (Table 8).

MaxEnt environmental niche modeling

Univariate models

Forty-four environmental and landscape covariates (Table 9) were tested independently in MaxEnt (Table 10). The covariates that produced the models with the highest accuracy (AUC) were max temperature of the warmest month (AUC= 0.912), temperature annual range (AUC= 0.912), and August average solar radiation (AUC= 0.912). The covariates that produced the models with the lowest accuracy were imperviousness (AUC= 0.504), minimum temperature of the coldest month (AUC= 0.675), and June average precipitation (AUC= 0.702).

Multi-variate models

Average AUC for the environmental niche models was 0.901. The land-scape only model (M1, Fig. A24) revealed elevation to be a strong limiting factor for *B. balteatus*, with this variable having the strongest influence on the model, as indicated by percent contribution (88.7%), highest gain when used in isolation, and greatest decrease in gain when excluded. The climate-only model that excluded positively correlated variables (M2, Fig. A25) revealed mean temperature of the wettest quarter (BIO8) to have the strongest influence on the final model (percent contribution = 66.7%). Incorporating non-correlated landscape variables into this model (M3, Fig. 8) produced the model with the highest accuracy in predicting *B. balteatus* distribution (AUC= 0.923) (Table 11). This model revealed BIO8 to again have the strongest influence on the final model (percent contribution = 54.7%), followed by temperature seasonality (BIO4, percent contribution = 17%), and land-use (percent contribution = 9.4%). When adding elevation into this same model (M4, Fig. A26),

elevation had the strongest effect on *B. balteatus* distribution (percent contribution = 51.3%), followed by BIO 8 (percent contribution = 21.5%) and BIO4 (percent contribution = 12.6%).

The model that included climate variables hypothesized a priori to affect *B. balteatus* gene flow (M5, Fig. A27) revealed the max temperature of the warmest month (BIO5) to have the strongest influence on the model (percent contribution = 73.%), followed by annual precipitation (BIO12, 9.5%), and mean temperature of the wettest quarter (BIO8, 6.2%). Elevation was hypothesized a priori to be the landscape variable that would most influence gene flow of *B. balteatus*, and incorporating this into the model (M6, Fig. A28) increased model accuracy.

The model that incorporated June, July and August average monthly climate data (M7, Fig. A29) revealed August maximum temperature to be a strong limiting factor for *B. balteatus*, with this variable having the highest percent contribution to the model (48.6%), followed by August solar radiation (28.9%), and July vapor pressure (3.1%). After removing positively correlated variables (M8, Fig. A30), August vapor pressure had the highest percent contribution to the model (64%), followed by July solar radiation (31%), and August average precipitation (2.5%).

The model that combined all uncorrelated variables (M9, Fig. A31) revealed August vapor pressure to again have the highest contribution to the model (49%), followed by July solar radiation (16.3%), and temperature seasonality (9.7%). The model that combined all forty-four variables (M10, Fig. A32) revealed August maximum temperature as having the strongest influence on the model (percent contribution = 37.3%), followed by annual precipitation seasonality (BIO12, 7.9%), and precipitation of the driest quarter (BIO19, 7.2%).

Any model that included landscape variables always revealed elevation to be one of the top contributing factors, while imperviousness always had the weakest influence on the model (percent contribution was never more than 2% in any model). Incorporating climate variables into the models increased model accuracy, with the highest performing model (M3) including uncorrelated bioclimatic and landscape variables (AUC= 0.923). The lowest performing models only included landscape variables (M1, AUC= 0.868) or only incorporated uncorrelated monthly climate variables (M8, AUC= 0.867). Incorporating more variables did not necessarily increase model accuracy or ability to predict species distribution (M9, AUC= 0.911; M10, AUC= 0.903).

Potential dispersal pathways and landscape connectivity

Circuitscape analyses predicted that gene flow patterns vary across the species' range in the central Rocky Mountains, with unique combinations of landscape and climatic variables affecting gene flow in different areas. Across all models, sites in the central portions of the study area had very little resistance between them (Mt. Democrat, Boreas Mtn., Horseshoe Mtn., Pennsylvania Mtn., and Mt. Silverheels). This is indicated by the high number of dispersal pathways connecting these sites, which is largely facilitated by high elevation ridgelines (Fig. 9). The Boreas and Silverheels sites had the highest amount of dispersal pathways between them, as they are directly connected by a small ridgeline. The Democrat, Penn, and Horseshoe sites also exhibit high connectivity and are also all connected by a long ridgeline. There are fewer pathways that connect these two areas, which are separated by a major highway and two small towns, indicating that dispersal may be limited.

The northeast corner of the study region (Niwot Ridge and Mt. Evans) had moderate levels of dispersal pathways connecting them to the rest of the study sites, with a network of high elevation ridgelines facilitating dispersal between these areas. Most models revealed that Mt. Evans is connected to the central region of the study area by a lower level of dispersal pathways that follow along high elevation ridgelines; however, there is a low elevation valley with a highway that prevents these two regions from being completely connected and may limit gene flow between these regions. All of the models reveal the northernmost site, Niwot Ridge, to be least connected via dispersal pathways to the rest of the study region. There are high levels of connectivity directly south of this site, but connectivity is limited to the west of this area by urban areas and lower elevation forests.

Near the southwestern portion of the study area (Mt. Elbert and Mt. Quail), gene flow was more restricted overall, with most models revealing relatively fewer dispersal pathways connecting these sites to the rest of the study region. Some models show large gaps in the landscape with very few dispersal pathways (M1, M4, M10), while M2 shows absolutely no dispersal pathways between these regions. This indicates that there is far less facilitation of dispersal by connected ridgelines and more limitation by low elevation, forested valleys. This area is also separated from the other study sites by a major highway that spans approximately 115 km through the study region, which may function as a linear barrier to gene flow. Most models revealed that the Elbert and Quail sites were buffered by high levels of dispersal pathways, however dispersal directly between them is limited. A low elevation, forested valley and major highway also intersect these sites, further demonstrating that dispersal may be limited by these landscape factors.

Landscape connectivity was completely limited in the southeast portion of the study region, which is primarily privately owned land that is predominantly for ranching and mining. All of the models also revealed a large gap in connectivity that lies north of the direct center of the study area, which is a predominantly urban area comprised of four cities. These regions are lower in elevation compared to much of the study region (<3,000 m). Limited connectivity may indicate that anthropogenic changes in the landscape function as barriers to dispersal.

Estimating Isolation by Resistance

Just as population structure indicated low levels of genetic differentiation among populations, landscape genetic analyses revealed signatures consistent with gene flow among regions. The univariate models with the highest correlation to genetic data were temperature seasonality ($R^2 = 0.0520$), temperature annual range ($R^2 = 0.0523$), and June average precipitation ($R^2 = 0.0612$) (Table 10). The univariate models with the lowest correlation to genetic data were annual mean precipitation ($R^2 = 0.0001$), and June, July, and August minimum temperature ($R^2 = 0.0003$, 0.0002 , and 0.0003 , respectively). All multi-variate models resulted in non-significant relationships to the genetic distance data (Table 8; Fig. 10).

DISCUSSION

I assessed levels of genetic differentiation among populations of *B. balteatus* in the central Rocky Mountains and assessed how a heterogeneous landscape contributes to the genetic structure of this alpine species. I identified: a) the population genetic structure among *B. balteatus* subpopulations using microsatellite markers; b) the first regional geographical

distribution for *B. balteatus* in the central Rocky Mountains and which environmental factors may be limiting distribution in the study area; and c) the pathways within the study area where the landscape may facilitate dispersal and gene flow between populations of *B. balteatus*. This study helps provide an understanding of landscape permeability for an alpine bumble bee that is located at high elevations within a largely unsuitable matrix of lowland habitat.

Specifically, I tested the hypotheses that (i) populations that are separated by large geographic distances or that are not connected by areas of suitable habitat will show reduced genetic diversity and higher levels of inbreeding than populations that are closer together geographically and that share connected areas of suitable habitat, (ii) incorporating multiple landscape and environmental factors into models would better improve the fit of models to genetic data, and (iii) models of isolation by resistance would perform better in genetic comparisons than traditional models of isolation by distance.

Population genetics

Nearly half of all populations across all loci deviated from Hardy-Weinberg expectations and 4 loci pairs exhibited significant linkage disequilibrium, which could be a result of genotyping errors or null alleles, however these errors typically affect only a select number of loci, so it is instead likely that these deviations indicate inbreeding or genetic structure. Inbreeding was present in most populations which is likely due to a significant homozygote excess among almost all populations. Overall observed heterozygosity was much lower than was expected, which could indicate reduced gene flow among populations. Bumble bees are particularly susceptible to inbreeding due to their low effective population sizes, low genetic variation from haplo-diploidy, and their monoandrous mating system

(Darvill et al. 2006). Although colonies can contain upwards of 200 workers, only one reproductive queen is responsible for producing all the offspring, meaning that even apparently abundant populations may actually have limited genetic diversity and may be more vulnerable to stochastic effects (Dreier et al. 2014).

Population differentiation

The results show significant genetic differentiation between most population pairs (28 out of 36 pairs, $P < 0.04$). Although overall F_{ST} was low ($F_{ST} = 0.019$), the pattern of pairwise F_{ST} and the results from the cluster analysis both support the presence of distinct genetic groups. Analysis of genetic clusters suggests that there are six distinct genetic groups present when using $LnP(D)$ estimates and 3 distinct genetic groups when using delta K estimates, however the bar plots (Fig. 3) for both estimates suggest that the genetic structure among these populations is primarily segregated into two clusters. The northernmost site, Niwot, appears to be more related to the lower sites (Silverheels, Horseshoe, and Penn) than to the upper sites which are located in closer proximity. This pattern is similar for one of the southernmost sites, Elbert, which appears to be more related to sites that are farther away geographically (Democrat, Boreas, and Silverheels) than to those that are closest to it (Quail, Horseshoe, Penn). Pairwise F_{ST} results support this; Niwot is more genetically differentiated from the most proximal sites ($F_{ST} = 0.0352$ - 0.0418) compared to those that are farther away ($F_{ST} = 0.0042$ - 0.0052), however all pairwise estimates were significant ($.0014 < P < 0.0139$).

Interestingly, the sites that were closest together geographically exhibited some of the highest genetic differentiation; Democrat and Penn are less than 9 km apart and yet pairwise F_{ST} was .02965; Boreas and Silverheels are also less than 9 km apart and $F_{ST} = 0.03543$; and Democrat and Silverheels are less than 12 km apart and were most genetically dissimilar (F_{ST}

= 0.04349). My results also found that populations of *B. balteatus* as far apart as 109 to 134 km (Niwot to Horseshoe and Niwot to Quail) were less genetically differentiated (F_{ST} = 0.00522 and F_{ST} = 0.01027, respectively). These patterns of pairwise differentiation and the lack of support for isolation by distance (IBD) (R^2 = 0.0035) suggest that geographic distance alone is not sufficient to explain patterns of genetic variation.

Bumble bee dispersal is not likely to be limited by geographic distance alone, but rather influenced by the complexity of the landscape (Goulson et al. 2011; Lozier et al. 2013; Jha and Kremen 2013; Jha 2015; Bartlett et al. 2016; Penado et al. 2016). A study examining *B. bifarius*, which is a species that co-occurs with *B. balteatus* in much of its range, found that populations in Western North America were largely influenced by variation in habitat suitability (Lozier et al. 2013). Dry intervening basins and deserts limited dispersal for *B. bifarius*, while forested mountain ranges were strongly associated with greater habitat suitability (Lozier et al. 2013). Populations at higher elevations exhibited more genetic differentiation than those that were found in more homogeneous landscapes at lower elevations, as they were connected by narrower bands of suitable habitat compared to the lowland populations (Lozier et al. 2013). As the complexity of the landscape increases, dispersal and gene flow are better predicted by habitat quality and spatial heterogeneity than by distance alone. In other words, Isolation by Resistance (IBR) models should improve the relationship with genetic distance compared to traditional models of Isolation by Distance (IBD).

As *B. balteatus* is an alpine bumble bee and was collected at elevations ranging from 3,743 – 4,012 m, I predicted that including elevation information would improve models that predict gene flow for this species. Surprisingly, the IBR models that included elevation did

not significantly improve the relationship to genetic differentiation ($R^2 = .0066$). These results are similar to other studies that have used IBR models to predict dispersal and gene flow for bumble bees and also found that elevation did not improve the model fit (Bartlett et al. 2016; Goulson et al. 2011; Jha and Kremen 2013). However, incorporating elevation into the environmental niche models (ENM) did improve model accuracy and elevation was always the highest contributing landscape variable in terms of percent contribution. Consistent with the MaxEnt results, connectivity modeling always predicted high levels of dispersal pathways along high elevation ridgelines, while lower elevation valleys always limited connectivity between populations. This finding indicates that elevation is still likely a good predictor of *B. balteatus* distribution, even though it did not improve IBR model fit.

Studies examining other landscape factors have found that incorporating ocean bathymetry (Goulson et al. 2011), ocean area (Darvill et al. 2010; Jha 2015), impervious cover, and land use (Jha 2015; Jha and Kremen 2013) can significantly improve models of genetic differentiation and gene flow. These landscape variables can function as barriers to dispersal and can influence population genetic structure at broad spatial scales. Incorporating land-use into resistance models for this study did not necessarily increase model fit for IBR analyses, but ENM models revealed that barren land, high rocky outcrops, and areas with perennial ice and snow were the most suitable areas of habitat for *B. balteatus*. Forests and developed land were the least suitable areas of habitat, indicating that these low elevation areas may function as landscape barriers for a high elevation bumble bee. Incorporating imperviousness into ENMs did not improve model accuracy as it was always the variable that had the lowest percent contribution for MaxEnt model. However, resistance surfaces revealed that major highways may act as barriers to dispersal for *B. balteatus*. With that said,

these major highways may have an inhibitory effect on dispersal because they are also located at lower elevations.

Along with including landscape information into the models, I predicted that incorporating bioclimatic information would improve models that predict gene flow for *B. balteatus*. Indeed, the multi-variate model that only incorporated landscape variables had the lowest model accuracy in predicting *B. balteatus* distribution, while the model that included uncorrelated bioclimatic variables with landscape variables had the highest model accuracy. This model predicted high habitat suitability to be in areas with suitable average temperatures during the wet and dry seasons (BIO 8 and 9, respectively), high rocky outcrops (land-use), and low tree canopy cover.

The next best performing multi-variate model included only bioclimatic variables that are considered to be biologically relevant to bumble bees; bees need suitable year round temperatures and levels of precipitation for floral resources, nesting sites, and overwintering habitats, therefore annual precipitation and average, maximum, and minimum temperatures were included in this model. A similar study on a co-occurring species used these same model covariates to measure landscape effects on gene flow found very similar results; annual precipitation, maximum temperature of the warmest month, and average temperature of the wettest quarter were the strongest limiting factors for *B. bifarius* populations in the western US (Lozier et al. 2013). *B. balteatus* and *B. bifarius* overlap in much of their distributions and therefore may have dispersal and gene flow limitations from the same environmental factors.

Several environmental niche models were developed in this study to find the best combination of environmental and landscape variables that could explain *B. balteatus* gene

flow and dispersal. Individual covariates were tested for their effects on *B. balteatus*' distribution and multi-variate models varied in complexity, ranging from four to forty-four variables. Monthly climate variables were included in some of the models in order to reflect the environmental conditions in the three months in which *B. balteatus* is most active: June, July, and August. *B. balteatus* queens emerge from hibernation in mid-June and must immediately search for floral resources to replenish her diet and begin founding her colony. Throughout all of July, the queen is producing as many female worker offspring as possible, so peak worker abundance is dependent on suitable temperatures and precipitation for enough floral resources to maintain colony growth. In August, the queen begins producing new reproductives, which require more resources than worker bees, so suitable climatic conditions are necessary towards the end of the season to ensure enough reproductives will survive and mate. Including these variables into a model revealed August maximum temperature and solar radiation to be the highest contributing variables. These two variables are likely highly correlated, however; so producing a model after removing correlated variables revealed August vapor pressure and July solar radiation to be the highest contributing variables to *B. balteatus* distribution in the summer.

Bumble bees need suitable year-round precipitation in the form of snow pack to insulate overwintering hibernation sites. If there is insufficient snow to insulate her overwintering site, a queen may emerge out of hibernation too soon, without enough floral resources, or she may not emerge at all. Although this study did not model winter monthly climate conditions, it would be useful to consider these environmental factors in the future in order to predict habitat suitability and connectivity for the queens who must survive almost an entire year.

Using these environmental niche models to produce resistance surfaces revealed that several areas of unsuitable habitat exist within this study area. All of the models revealed major highways to be highly resistant to gene flow; visible gaps between sites occur along these roads. Very limited, if any, dispersal pathways existed across the southwest portion of the study area that connected the southernmost sites to the central study region and a major highway dissects this region. To the southeast, every model revealed that there were no dispersal pathways across areas that are predominantly ranches and mines, indicating that anthropogenic forces may influence dispersal among populations. With this said, all of these areas of unsuitable habitat occur at much lower elevations (<2,800 m), which may be the largest inhibitor of dispersal and gene flow for an alpine bumble bee.

A surprising find in this study was that no resistance surface improved the IBR relationship with genetic differentiation. Linear regression and mantel tests revealed that no single covariate nor multi-variate model significantly improved the correlation to genetic distance data over traditional isolation by distance models. Although MaxEnt environmental niche models and CIRCUITSCAPE connectivity models visually represented habitat suitability and connectivity well, no significant relationship to genetic variation among *B. balteatus* populations was found.

There are likely several explanations for these non-significant relationships; first, the available contemporary bioclimatic variables are yearly and monthly averages from 1970-2000. Temperatures in the Rocky Mountains have increased over 2°C in the past few decades (Manino et al. 2007), so using climate data from over 30 years ago likely do not reflect the average temperatures at which the specimens for this study were collected. Increased temperatures have caused earlier snowmelt and decreased snow pack (Diaz et al. 2014) and

have also influenced floral abundance above tree line (CaraDonna et al. 2014), which also indicates that the precipitation data likely do not reflect identical conditions as during data collection. Second, there are environmental and landscape conditions that were not included in these models that are also very likely to affect *B. balteatus* distribution and environmental niche: wind direction, rather than just speed, may influence long-distance dispersal events such as queens and males dispersing for mates, or short-distance dispersal such as workers foraging for resources; floral abundance and nesting sites are direct resource limitations for bumble bees, yet data for these factors are largely unavailable. Lastly, although the occurrence records from the Global Biodiversity Information Facility (GBIF) index provide useful information on *B. balteatus* occurrences, there is some inherent uncertainty in these records and their use in distribution models may influence niche estimates if the data are inaccurate.

A historical perspective may provide an explanation for patterns of genetic differentiation observed that cannot be explained by current observable habitat features. Apparent disjunct populations seen in genetic structure analyses may have been two distinct populations that resulted from geographic isolation in the distant past. Candidate episodes might include Pleistocene glaciation or some catastrophic event such as a wildfire. Later, when suitable habitat became available between the disjunct sites, repopulation occurred via dispersal from the two genetically differentiated areas. If this explanation were the case, it is not clear why subsequent gene flow would not have homogenized the populations, given the apparent ample dispersal pathways predicted.

Although IBR and IBD models did not explain patterns of genetic variation among populations of *B. balteatus* for this study, it is important to continue mapping and modeling

species distributions, particularly for those that are ecologically significant. The low pairwise genetic differentiation estimates and moderate to high heterozygosity suggest that these populations may be stable and can withstand environmental challenges in a complex landscape, or it could be too early to detect any appreciable decrease in genetic diversity due to genetic drift. Likewise, the inbreeding estimates among *B. balteatus* populations may be a result of population structuring, or they may be the early signals that these populations may be at risk for loss of genetic diversity and inbreeding depression, which could seriously influence the persistence of these wild populations of bumble bees. Bumble bee habitat is becoming more fragmented at the landscape scale (Goulson et al. 2008) which could result in the isolation of populations and even extinction in the face of further environmental changes.

These results suggest that conservation management strategies for *B. balteatus* may require corridors of connected and continuous suitable habitat along high elevation ridgelines in the central Rocky Mountains. Connectivity modeling revealed these areas as likely to facilitate dispersal and gene flow and therefore they may be of particular value for the persistence of *B. balteatus* and other alpine bumble bees in Western North America. In the future it may be beneficial to examine the entire distribution of *B. balteatus* in order to elucidate landscape effects on genetic variation at the larger scale. More samples collected regionally within the study area may also prove beneficial in understanding *B. balteatus* population connectivity and may foster insight into more dispersal pathways across an extremely heterogeneous landscape. The alpine environment is fragile, yet one of the most biodiverse regions in the world, and the climate above tree line is changing rapidly. In the last thirty years, bee morphology has also changed dramatically in response to reduced floral resources. If dispersal pathways remain connected and adequate habitat remains protected, *B.*

balteatus may be able to rapidly adapt to novel challenges above tree line and persist despite climate change.

Tables

Table 1 $N_{(sample\ size)}$ number of individuals sampled from each site, $N_{(genotyped)}$ number of individuals successfully genotyped, $N_{(colonies)}$ number of colonies at each site

Population	$N_{(sampled)}$	$N_{(genotyped)}$	$N_{(colonies)}$
Democrat	96	81	72
Boreas	41	34	32
Horseshoe	55	46	43
Evans	51	50	48
Penn	48	35	34
Quail	41	38	33
Niwot	45	45	42
Silverheels	52	48	39
Elbert	16	15	15
Total	446	392	358

Table 2 Size range in base pairs and number of alleles for each microsatellite locus

Locus	Size range	No. alleles
B124	222-242	15
BTERN01	109-154	16
BT10	125-152	18
BL11	122-134	13
BL13	152-192	19
B10	179-201	14
BT28	174-186	4
B96	221-251	21
Average		15

Table 3 Standard measures of genetic diversity for each population: H_E expected

heterozygosity, H_O observed heterozygosity, AR allelic richness, F_{IS} inbreeding coefficient

Population	H_E	H_O	AR	F_{IS}
Democrat	0.793	0.755	9.23	0.049
Boreas	0.824	0.701	9.58	0.149
Horseshoe	0.797	0.709	8.56	0.110
Evans	0.804	0.679	9.36	0.155
Penn	0.827	0.720	9.66	0.129
Quail	0.824	0.803	8.96	0.025
Niwot	0.784	0.765	8.39	0.025
Silverheels	0.801	0.647	9.39	0.192
Elbert	0.830	0.725	9.88	0.127
Total	0.809	0.723	9.22	0.107

Table 4 Pairwise F_{ST} values are below the diagonal, pairwise significance above the diagonal, significant values are in bold ($p < 0.05$).

	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert
Democrat	–	0.06111	0.00139	0.15556	0.00139	0.0014	0.0014	0.00139	0.1819
Boreas	0.0124	–	0.00139	0.23194	0.00139	0.0014	0.0014	0.00139	0.3056
Horseshoe	0.0285	0.024	–	0.00139	0.01389	0.0014	0.0139	0.00139	0.0028
Evans	0.0001	0.0055	0.0238	–	0.00139	0.0014	0.0014	0.00139	0.3333
Penn	0.0291	0.0245	0.0032	0.0223	–	0.0389	0.0014	0.29167	0.0181
Quail	0.0392	0.0311	0.0108	0.0289	0.0024	–	0.0014	0.03333	0.0014
Niwot	0.0418	0.0389	0.0052	0.0352	0.0042	0.0103	–	0.07917	0.0014
Silverheels	0.0434	0.035	0.0082	0.0339	0.0028	0.0051	0.0001	–	0.0014
Elbert	0.0051	-0.0002	0.0093	0.0019	0.008	0.0175	0.0233	0.0192	–

Table 5 Standard estimates of gene diversities and differentiation by locus. H_E expected heterozygosity, H_O observed heterozygosity, H_T total gene diversity, F_{IS} Wright's estimate of inbreeding coefficient, F_{ST} Wright's fixation index, G_{ST} the F_{ST} analog adjusted for bias, and G'_{ST} Nei's multi-allelic estimation. $P(x)$ indicates probabilities for the statistics, significant values are in bold

Locus	H_E	H_O	H_T	F_{IS}	$P(F_{IS})$	F_{ST}	$P(F_{ST})$	G_{ST}	$P(G_{ST})$	G'_{ST}	$P(G'_{ST})$
B124	0.814	0.718	0.875	0.101	1.000	0.094	0.001	0.071	0.001	0.079	0.001
BTERN01	0.891	0.765	0.895	0.127	0.140	0.004	0.080	0.004	0.080	0.004	0.080
BT10	0.859	0.723	0.865	0.152	0.477	0.009	0.026	0.007	0.026	0.008	0.026
BL11	0.870	0.724	0.871	0.151	0.090	0.003	0.357	0.001	0.376	0.001	0.376
BL13	0.880	0.849	0.897	0.035	0.980	0.021	0.001	0.019	0.001	0.021	0.001
B10	0.769	0.678	0.776	0.132	0.931	0.008	0.021	0.009	0.017	0.010	0.017
BT28	0.487	0.443	0.489	0.079	0.452	0.009	0.235	0.005	0.240	0.005	0.240
B96	0.902	0.881	0.908	0.029	0.921	0.007	0.018	0.006	0.017	0.007	0.017
Overall	0.809	0.723	0.822	0.101	0.990	0.019	0.001	0.016	0.001	0.018	0.001

Table 6 Population pairwise F_{ST} ($F_{ST}/(1-F_{ST})$ values are displayed below the diagonal, pairwise Euclidean distances (km) displayed above the diagonal

	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert
Democrat	0	18.06	17.57	50.84	8.33	41.95	91.9	11.59	36.15
Boreas	0.01275	0	31.9	33.11	22.93	57.85	78.18	8.91	53.55
Horseshoe	0.02867	0.02406	0	64.63	9.55	26.59	108.88	23.07	23.7
Evans	0.0001179	0.00607	0.02425	0	55.98	90.63	52.61	41.64	86.66
Penn	0.02965	0.02481	0.003401	0.02301	0	35.06	99.36	14.42	30.87
Quail	0.03922	0.03115	0.01075	0.02937	0.0024	0	133.87	49.06	11.8
Niwot	0.04184	0.03935	0.00522	0.03594	0.0042	0.01027	0	86.91	126.81
Silverheels	0.04349	0.03543	0.008232	0.03447	0.0027	0.00507	6E-05	0	45.28
Elbert	0.005149	-0.000055	0.0093	0.00199	0.0082	0.01747	0.02334	0.01923	0

Table 7 Population pairwise F_{ST} ($F_{ST}/(1-F_{ST})$ values are displayed below the diagonal, logarithm of Euclidean distance (km) displayed above the diagonal

	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert
Democrat	—	0.219184	0.335206	0.633768	0.334468	0.440145	0.811750	0.278896	0.449920
Boreas	0.012913	—	0.136085	0.619195	0.136018	0.340928	0.897512	0.101679	0.347257
Horseshoe	0.029514	0.024651	—	0.723494	0.001606	0.249848	1.026080	0.188606	0.252884
Evans	0.000117	0.006107	0.024854	—	0.724385	0.959263	0.410473	0.535795	0.965008
Penn	0.030558	0.025445	0.003412	0.023549	—	0.248518	1.026500	0.189385	0.251592
Quail	0.040825	0.032149	0.010871	0.030258	0.002414	—	1.225900	0.426399	0.010823
Niwot	0.043665	0.040962	0.005246	0.037274	0.004216	0.010376	—	0.844017	1.234010
Silverheels	0.044020	0.035728	0.008058	0.034823	0.002506	0.005391	0.000730	—	0.431382
Elbert	0.005176	0.000056	0.009387	0.001994	0.008241	0.017776	0.023903	0.018149	—

Table 8 Linear regression (R^2) and Mantel test summaries that examine the effects of geographic distance, log of distance, and resistance distances on genetic differentiation

Model	R^2	Mantel r - value	P-value
$[F_{ST}/(1-F_{ST})] \sim \text{distance (km)}$.0035	-0.00411	0.7547
$[F_{ST}/(1-F_{ST})] \sim \log (\text{distance})$.0083	-0.00466	0.4970
$[F_{ST}/(1-F_{ST})] \sim \text{res M1}$	0.001	-0.00741	0.4949
$[F_{ST}/(1-F_{ST})] \sim \text{res M2}$.0219	-0.04411	0.7887
$[F_{ST}/(1-F_{ST})] \sim \text{res M3}$.0284	-0.03548	0.7260
$[F_{ST}/(1-F_{ST})] \sim \text{res M4}$.0178	-0.05027	0.8223
$[F_{ST}/(1-F_{ST})] \sim \text{res M5}$.0096	0.00093	0.4371
$[F_{ST}/(1-F_{ST})] \sim \text{res M6}$.0030	-0.01481	9.5511
$[F_{ST}/(1-F_{ST})] \sim \text{res M7}$.0132	-0.04615	0.7951
$[F_{ST}/(1-F_{ST})] \sim \text{res M8}$.0089	-0.04147	0.7491
$[F_{ST}/(1-F_{ST})] \sim \text{res M9}$.0151	-0.03548	0.7205
$[F_{ST}/(1-F_{ST})] \sim \text{res M10}$.0071	-0.04274	0.7730

Table 9 Bioclimatic, monthly climatic (June-August), and landscape variables used to create environmental niche models. Bioclimatic variables without collinearity problems are in bold

Bioclimatic variables	Monthly variables (June-August)	Landscape variables
Annual mean temperature (BIO1)	Minimum temperature (°C)	Elevation (m)
Mean diurnal range (BIO2)	Maximum temperature (°C)	Land use
Isothermality (BIO3)	Average temperature (°C)	Imperviousness
Temperature seasonality (BIO4)	Precipitation (mm)	Tree canopy cover
Max temperature of warmest month (BIO5)	Solar radiation (kJ m ⁻² day ⁻¹)	
Min temperature of coldest month (BIO6)	Wind speed (m s ⁻¹)	
Temperature annual range (BIO7)	Water vapor pressure (kPa)	
Mean temperature of wettest quarter (BIO8)		
Mean temperature of driest quarter (BIO9)		
Mean temperature of warmest quarter (BIO10)		
Mean temperature of coldest quarter (BIO11)		
Annual precipitation (BIO12)		
Precipitation of wettest month (BIO13)		
Precipitation of driest month (BIO14)		
Precipitation seasonality (BIO15)		
Precipitation of wettest quarter (BIO16)		
Precipitation of driest quarter (BIO17)		
Precipitation of warmest quarter (BIO18)		
Precipitation of coldest quarter (BIO19)		

Table 10 Univariate model results investigating MaxEnt model accuracy (AUC) and the relationship between genetic differentiation (F_{ST}) and resistance distance

Variable	AUC	MAXENT		CIRCUITSCAPE	
		Conduct R^2	Resist R^2	Conduct R^2	Resist R^2
Elevation	0.889	0.0007	0.0018	0.0066	
Land-use	0.713	0.0007	0.0001	—	—
Tree canopy cover	0.729	0.0156	0.0008	0.0147	—
Imperviousness	0.504	0.0095	0.0112	—	—
Annual mean precipitation	0.847	0.0001	0.0451	0.0181	—
Mean diurnal range	0.860	0.0420	0.0192	0.0027	0.0181
Isothermality	0.846	0.0222	0.0025	0.0085	0.0113
Temperature seasonality	0.813	0.0520	0.0183	0.0054	0.0155
Max temperature of warmest month	0.912	0.0092	0.0001	0.0090	0.0095
Min temperature of coldest month	0.675	0.0392	0.0002	—	—
Temperature annual range	0.912	0.0523	0.0219	0.0040	0.0170
Mean temperature of wettest quarter	0.857	0.0259	0.0557	—	—
Mean temperature of driest quarter	0.803	0.0165	0.0005	—	—
Mean temperature of warmest quarter	0.884	0.0010	0.0177	0.0184	0.0049
Mean temperature of coldest quarter	0.740	0.0050	0.0670	—	—
Annual precipitation	0.822	0.0305	0.0039	0.0148	0.0048
Precipitation of wettest month	0.795	0.0336	0.0013	0.0201	0.0025
Precipitation of driest month	0.808	0.0146	0.0002	0.0112	0.0072
Precipitation seasonality	0.825	0.0026	0.0653	0.0241	0.0051
Precipitation of wettest quarter	0.793	0.0476	0.0077	0.0242	0.0014
Precipitation of driest quarter	0.825	0.0150	0.0009	0.0096	0.1100
Precipitation of warmest quarter	0.811	0.0187	0.0040	0.0090	0.0117
Precipitation of coldest quarter	0.857	0.0098	0.0111	0.0073	0.0188
June minimum temperature	0.827	0.0003	0.0856	—	—
July minimum temperature	0.818	0.0002	0.0890	0.0613	0.0000
August minimum temperature	0.832	0.0003	0.0886	0.0700	0.0000
June maximum temperature	0.888	0.0052	0.0046	0.0133	0.0070
July maximum temperature	0.889	0.0091	0.0002	0.0090	0.0096
August maximum temperature	0.901	0.0088	0.0004	0.0094	0.0095
June average temperature	0.860	0.0010	0.0226	0.0027	0.0225
July average temperature	0.907	0.0011	0.0163	0.0171	0.0054
August average temperature	0.873	0.0009	0.0172	0.0184	0.0052
June average precipitation	0.702	0.0612	0.0059	0.0358	0.0001
July average precipitation	0.820	0.0071	0.0175	0.0072	0.0145
August average precipitation	0.793	0.0011	0.0439	0.0045	0.0216
June average solar radiation	0.776	0.0405	0.0297	0.0079	0.0123
July average solar radiation	0.897	0.0017	0.0000	0.0101	0.0099
August average solar radiation	0.912	0.0006	0.0016	0.0104	0.0096
June average vapor pressure	0.847	0.0006	0.0113	0.0203	0.0049
July average vapor pressure	0.871	0.0040	0.0025	0.0127	0.0078
August average vapor pressure	0.882	0.0075	0.0001	0.0106	0.0090
June average wind speed	0.903	0.0384	0.0163	0.0049	0.0153
July average wind speed	0.897	0.0467	0.0180	0.0045	0.0164
August average wind speed	0.854	0.0469	0.0220	0.0039	0.0172

Table 11 Analysis of MaxEnt environmental niche models used to estimate heterogeneity of habitat suitability for *B. balteatus*.

Model name	Model covariates	AUC
M1	Elevation, land-use, canopy cover, imperviousness	0.868
M2	BIO 3, 4, 6, 8, 9, 13	0.902
M3	M2 + land-use, canopy cover, imperviousness	0.923
M4	M3 + elevation	0.888
M5	BIO 1, 5, 6, 8, 9, 12, 13, 14	0.916
M6	M5 + elevation	0.918
M7	June, July, and August monthly climate averages	0.913
M8	Precipitation (6, 8), solar radiation (7), vapor pressure (8)	0.867
M9	M3 + M8	0.911
M10	Bio 1-19 + M1 + M7	0.903

Refer to Table 9 for variable explanations

Figure Legends

Figure 1 Distribution of alpine study sites in the central Rocky Mountains, Colorado, USA. Yellow points represent the survey sites. Counties are labeled and outlined in white. Green shading in the background represents elevation, with darker green representing lower elevation and white representing higher elevation. Inset shows study region outlined by the black square

Figure 2 Genetic clustering results for the determination of the number of genetic clusters (K) using (a) LnP(D) estimates and (b) delta K estimates. A star denotes the most likely number of clusters for each method

Figure 3 Genetic clustering results obtained for (a) six clusters and (b) three clusters. The x axis represents original populations: 1 Democrat, 2 Boreas, 3 Horseshoe, 4 Evans, 5 Penn, 6 Quail, 7 Niwot, 8 Silverheels, and 9 Elbert

Figure 4 Genetic clustering results obtained for six clusters. Each individual is represented by a thin vertical line divided into seven colored segments, with the length of each segment proportional to the estimated membership in each of the inferred 6 clusters

Figure 5 Neighbor joining genetic trees based on the net nucleotide distance between (a) six genetic clusters and (b) three genetic clusters

Figure 6 Isolation by distance: genetic differentiation ($F_{ST}/1 - F_{ST}$) as a function of geographic distance

Figure 7 Isolation by distance: genetic differentiation ($F_{ST}/1 - F_{ST}$) as a function of geographic distance (\log_{10})

Figure 8 *M3* Uncorrelated bioclimatic variables and landscape variables ENM

Figure 9 *M3* Uncorrelated bioclimatic and landscape variables resistance model. Gray square indicates study region

Figure 10 Isolation by resistance for the model including uncorrelated bioclimatic and landscape variables (*M3*). Dotted line indicates non-significant relationship

Figure 1

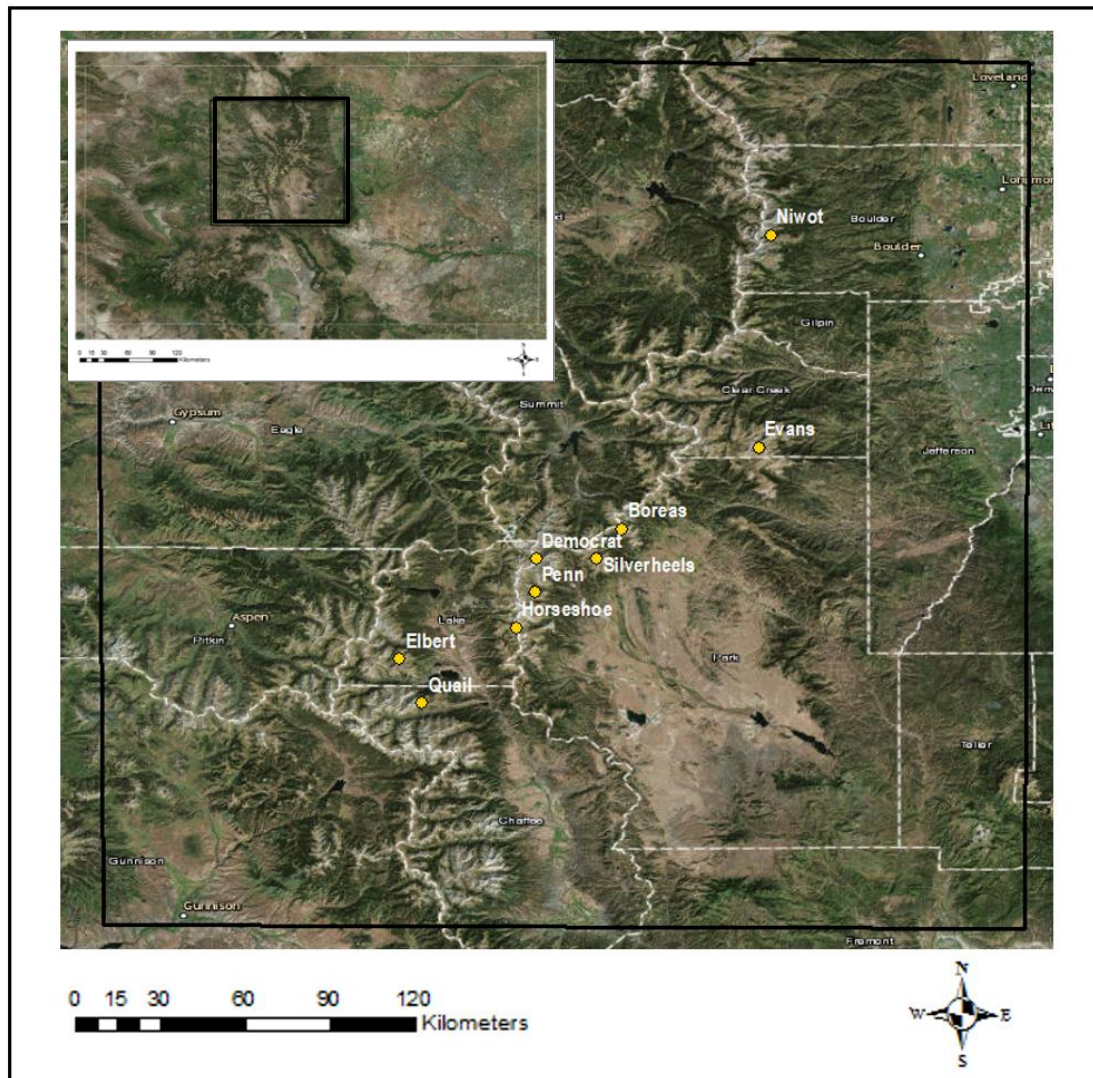


Figure 2

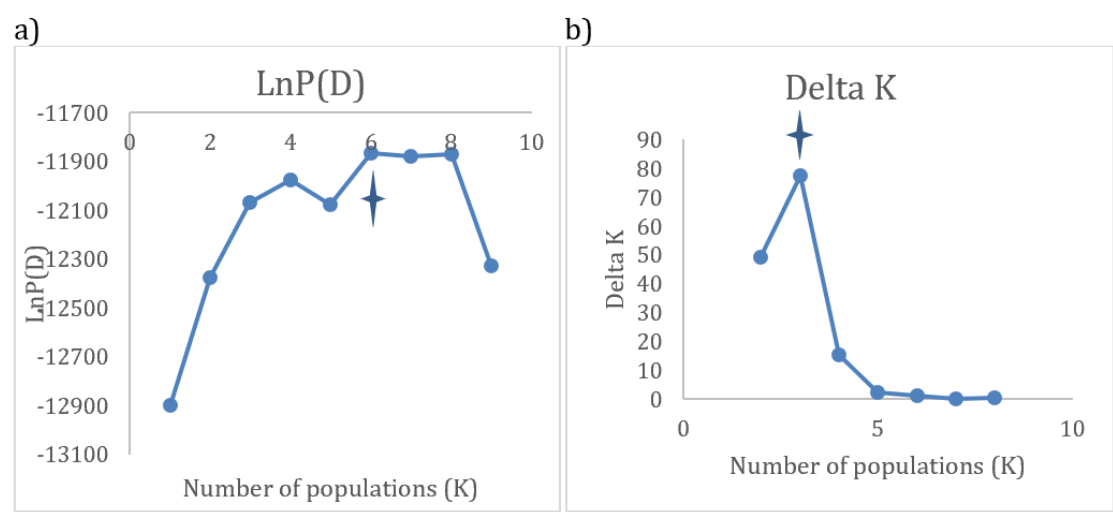


Figure 3

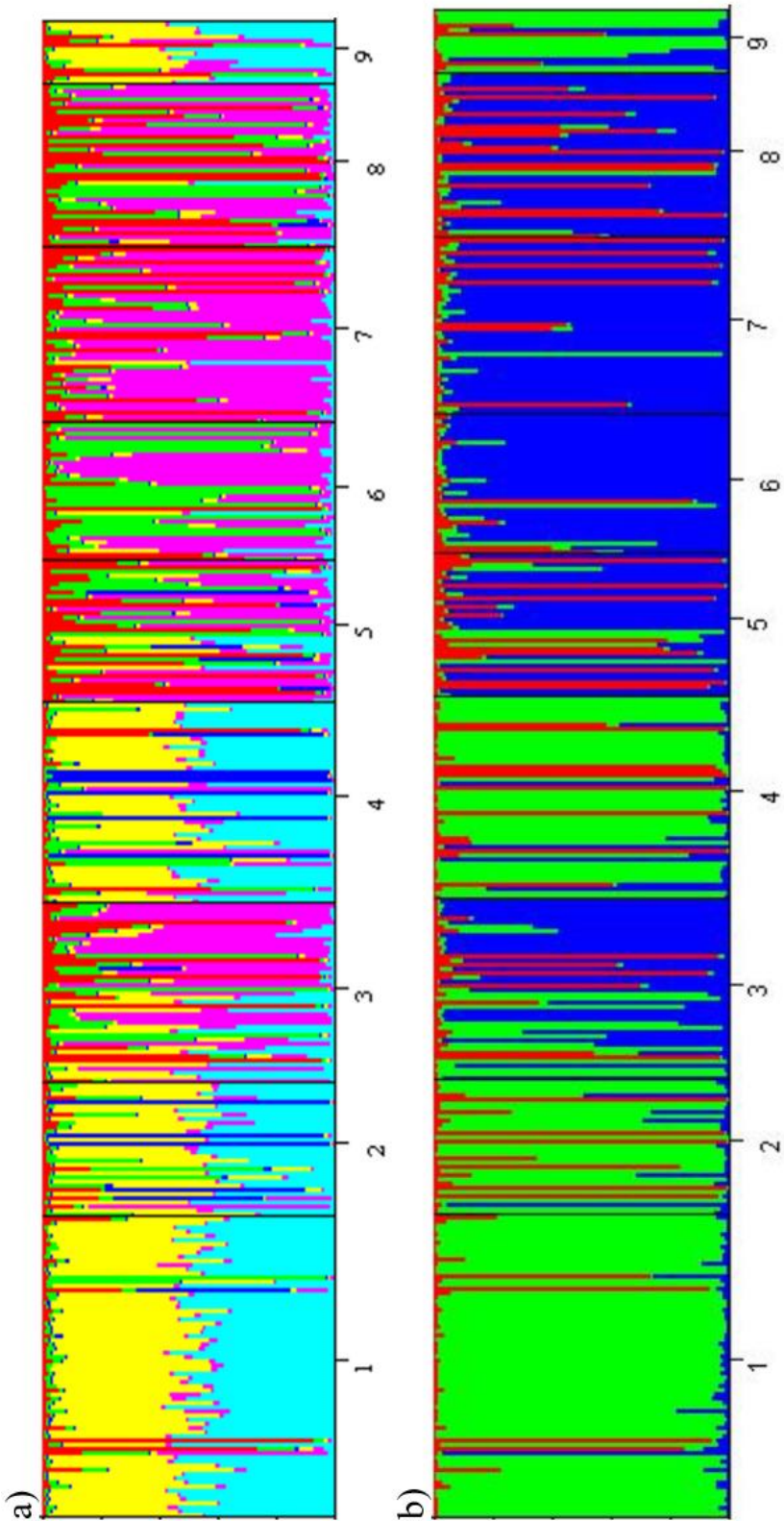


Figure 4

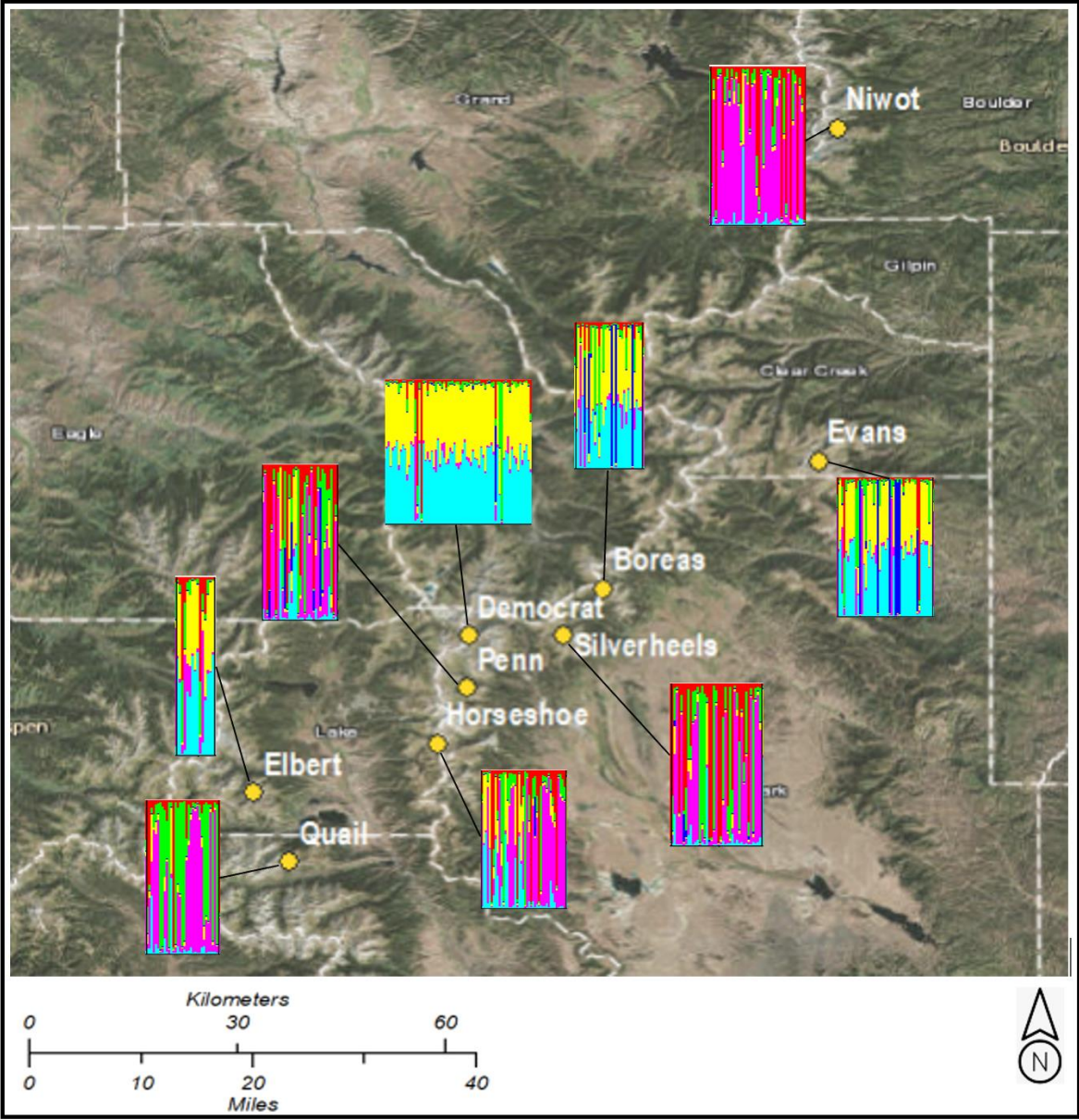


Figure 5

a)



b)



Figure 6

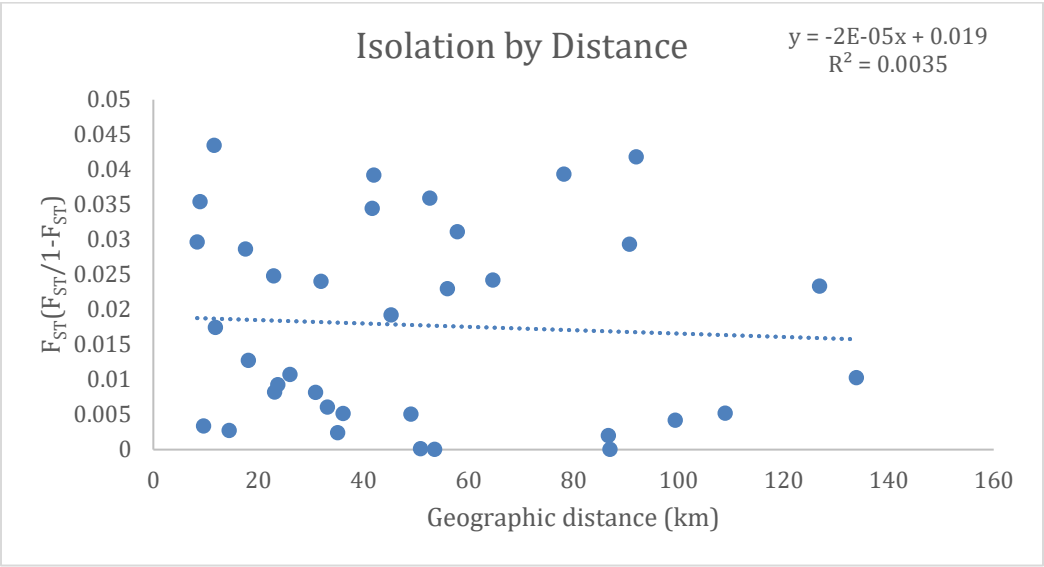


Figure 7

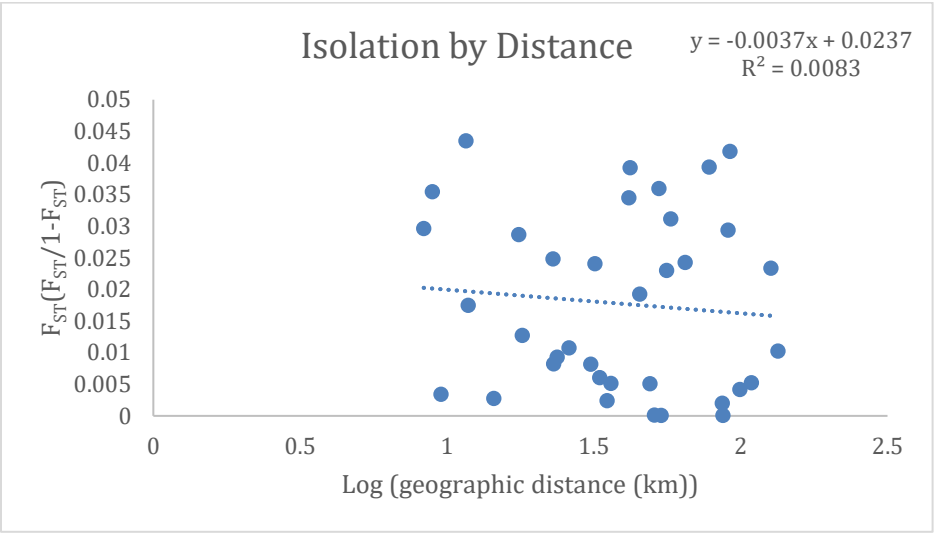


Figure 8

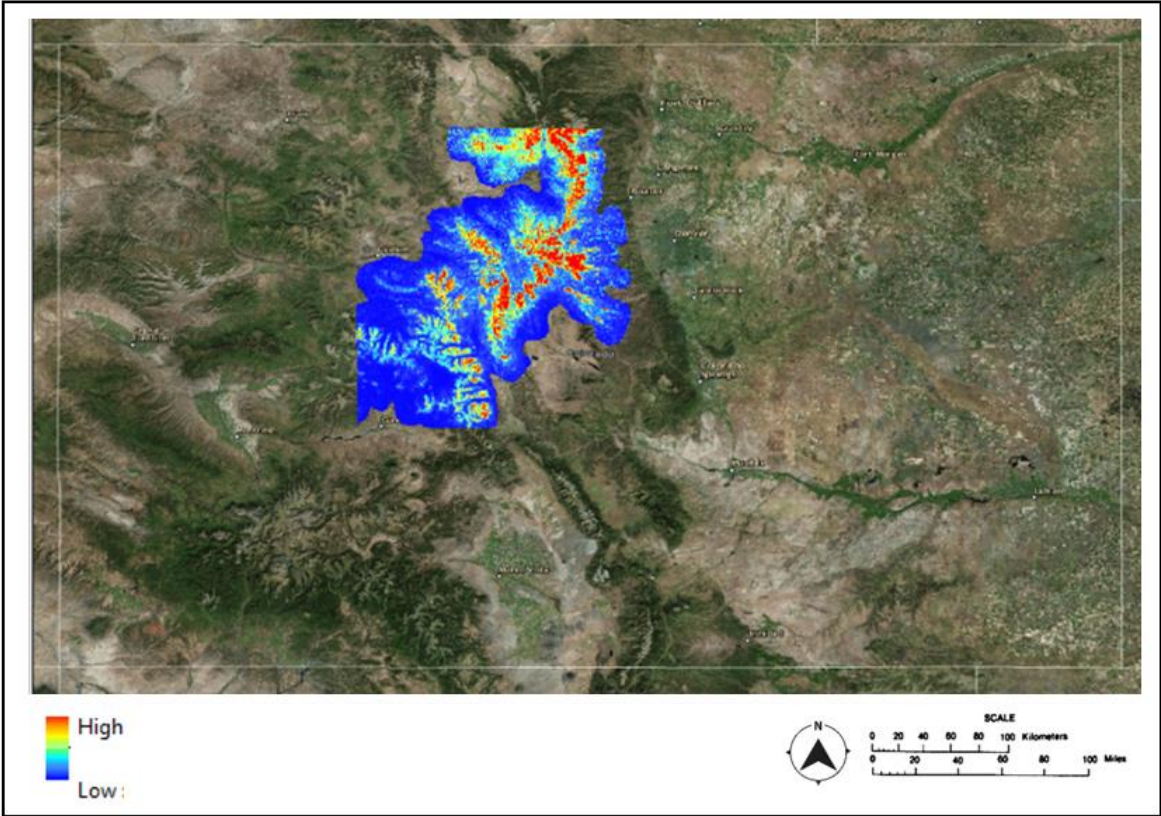


Figure 9

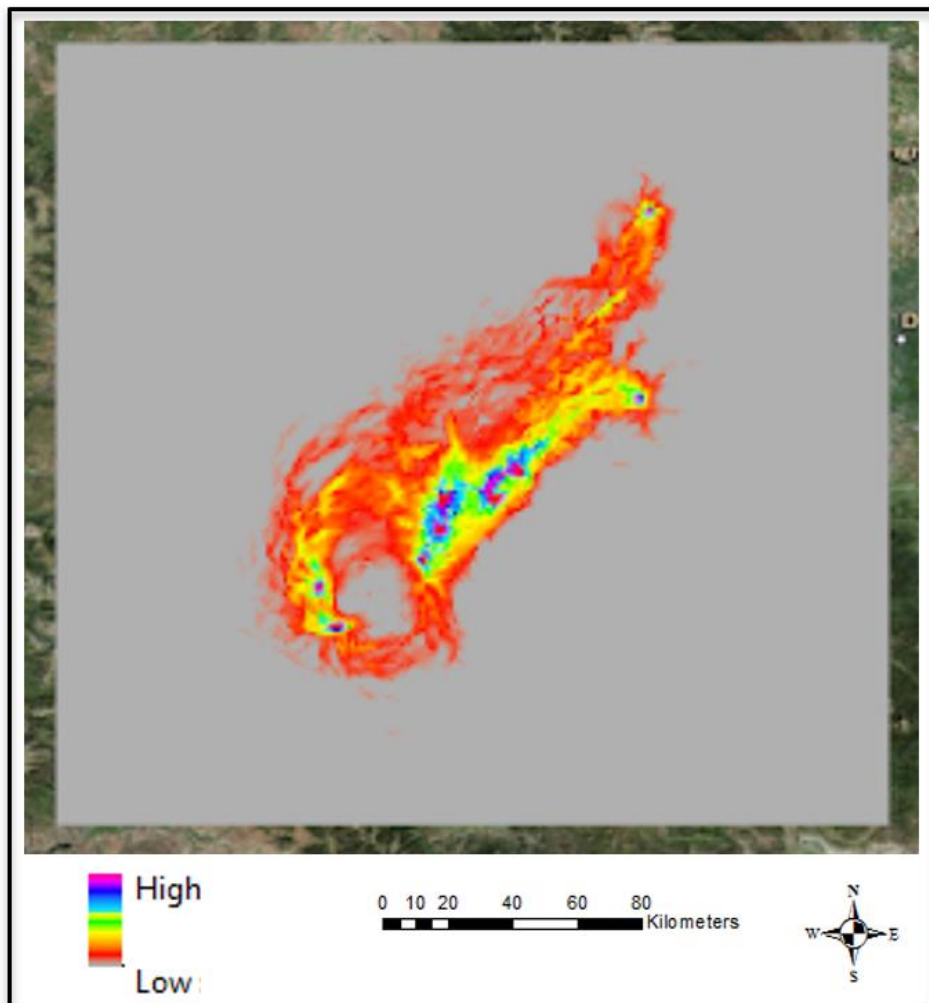
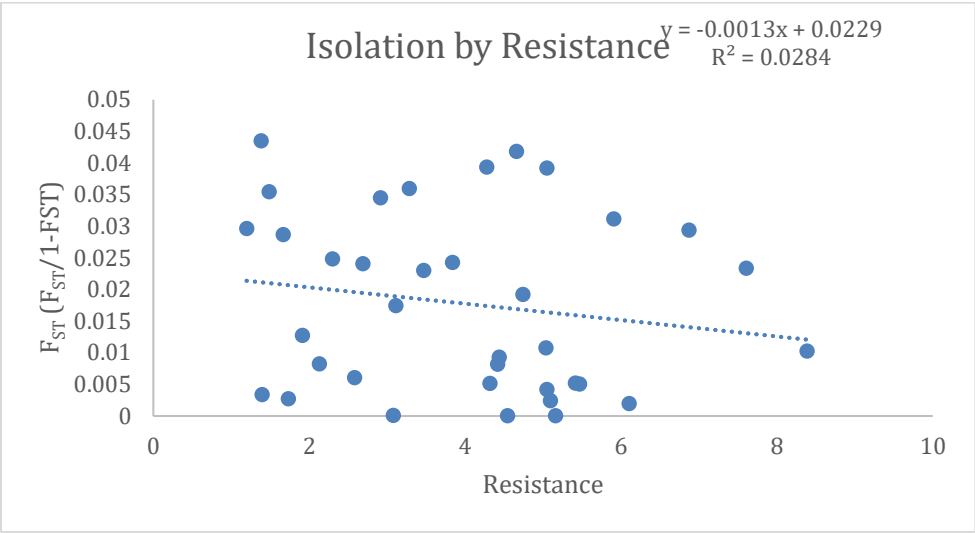


Figure 10



References Cited

- Adderley LJ, Vamosi JC (2015) Species and phylogenetic heterogeneity in visitation affects reproductive success in an island system. *Int J Plant Science* 176:186-196
- Aldridge S, Inouye DW, Forrest JRK, Barr WA, Miller-Rushing AJ (2011) Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *J Ecol* 99:905- 913
- Alvarado-Serrano DF, Knowles LL (2014) Ecological niche models in phyklogeographic studies: applications, advances, and precautions. *Mol Ecol Resour* 14:233-248
- Baguette M (2003) Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography* 26:153- 160
- Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Land Ecol* 22:1117-1129
- Bartlett LJ, Newbold T, Purves DW, Tittensor DP, Harfoot MJB (2016) Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proc. R. Soc. B* 283: 20161027
- Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *PNAS* 108(51): 20645-20649
- Billings WD (1989) Alpine vegetation. *Terrestrial vegetation of North America*: 392-420

- Billings WD, Mooney HA (1968) The ecology of arctic and alpine plants. *Biol Rev* 43:481-529
- Bommarco R, Lundin O, Smith HG, Rundlof M (2011) Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. B.* doi:10.1098/rspb.2011.0647
- Bourke AFG, Hammond RL (2002) Genetics of the scarce bumble bee, *Bombus distinguendus*, and nonlethal sampling of DNA from bumble bees. A Report for the RSPB
- Bowers (1985) Bumble bee colonization, extinction, and reproduction in subalpine meadows in Northeastern Utah. *Ecology* 66:914-927
- Brian MV (1965) *Social Insect Populations*. Academic Press, London.
- Braun CE (1980) Alpine bird communities of western North American: implications for management and research. *J Wildl Mgmt* 280-291
- Brown JH (1971) Mammals on Mountaintops: Nonequilibrium Insular Biogeography. *Amer Soc Nature* 105:467-478
- Byron PA (1980) Thesis. University of Colorado, Boulder
- Cameron SA, Hines HM (2007) A comprehensive phylogeny of the bumble bees (*Bombus*): BUMBLE BEE PHYLOGENY. *Biol J of Linn Soc* 91(1): 161-188
- Cameron S, Lozier JD, Strange JB, Koch JB, Cordes N, Solter LF, Griswold TL (2010) Patterns of widespread decline in North American bumble bees. *PNAS* 108:662-667

- CaraDonna PJ, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. *PNAS* 111(13): 4916-4921
- Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D (2006) Declines in forage availability for bumble bees at a national scale. *Biol Cons* 132:481-489
- Carvell C, Jordan WC, Bourke AFG, Pickles R, Redhead JW, Heard MS (2012) Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumble bee species. *Oikos* 121:734-742
- Chatterji S, Pachter L (2006) Reference based annotation with GeneMapper. *Genome Biol* 7 R29
- Chittka L, Williams NM, Rasmussen H, Thomson JD (1999) Navigation without vision: bumble bee orientation in complete darkness. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266:45-50
- Chen X, Shuai A, Inouye D, Schwartz, M (2015) Temperature and snowfall trigger alpine vegetation green-up on the world's roof. *Glob Change Biol* 3635-3636
- Colla SR, Gadallah F, Richardson L, Wagner D, Gall L (2012) Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodiv and Conserv* 21(14): 3585-3595
- Consortium for Integrated Climate Research in Western Mountains. United States Department of Agriculture Forest Service. July 2006.

- Cresswell JE, Osborne JL, Bell S (2002) A model of pollinator-mediated gene flow between plant populations, with numerical solutions for bumble bees pollinating oilseed rape. *Oikos* 98:375-384
- Darvill B, Ellis JS, Lye GC, Goulson D (2006) Population structure and inbreeding in a rare and declining bumble bee, *Bombus muscorum* (Hymenoptera: Apidae): Inbreeding in a rare bumble bee. *Mol Ecol* 15:601–611
- Darvill B (2007) The conservation genetics of the bumble bees *Bombus muscorum* and *Bombus jonellus* in a model island system. PhD thesis, University of Southampton.
- Darvill B, O'Connor S, Lye GC, Waters J, Lepais O, Goulson D (2009) Cryptic differences in dispersal lead to differential sensitivity to habitat fragmentation in two bumble bee species. *Mol Ecol* 19: 53-56
- Diaz HF, Millar CI (2004) Discussing the future of U.S. western mountains, climate change, and ecosystems. *Transactions of the American Geophysical Union* 85:329-330
- Diaz HF, Bradley RS, and Ning Liang (2014) Climatic changes in mountain regions of the American Cordillera and the Tropics: Historical Changes and Future Outlook. *Artic, Antarctic, and Alpine Research* 46(4): 735-743
- Dramstad WE (1996) Do bumble bees (Hymenoptera: Apidae) really forage close to their nests? *J Ins Behav* 2:163-182

- Dreier S, Redhead JW, Warren IA, Bourke AFG, Heard MS, Jordan WC, Carvell C (2014) Fine scale spatial genetic structure of common and declining bumble bees across an agricultural landscape. *Mol Ecol* 23:3384-3395
- Earl DA, VonHoldt BM (2012) Structure Harvester: a website for visualizing STRUCTURE output and implementing the Evanno method. *Cons Genet Res* 4:359-361
- Elith K, Phillips SJ, Hastie T, Miroslav D, Chee YE, Yates CJ (2010) A statistical explanation of MaxEnt for ecologists. *Div and Dist* 17(1): 43-57
- Ellis JS, Knight ME, Darvill B, Goulson D (2006) Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumble bee species, *Bombus sylvarum* (Hymenoptera: Apidae). *Mol Ecol* 15:4375-4386
- Estoup A, Slignac M, Cornuet J-M, Goudet J, Scholl A (1996) Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Mol Ecol* 5:19- 31
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol Ecol* 14:2611-2620
- Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* 164: 1567-1587
- Floyd CH, Van Vuren DH, May B (2005) Marmots on Great Basin Mountaintops: Using Genetics to Test a Biogeographic Paradigm. *Ecology* 86:2145-2153

- Forrest J, Inouye DW, Thomson JD (2010) Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? *Ecology* 91(2):431-440.
- Funk CR, Schmid-Hempel R, Schmid-Hempel P (2006) Microsatellite loci for *Bombus* spp. *Mol Ecol Notes* 6:83-86
- GBIF.org (February 29th 2016) GBIF Occurrence download. *Bombus balteatus* Dahlbom, 1832 in GBIF Secretariat (2017). GBIF Backbone Taxonomy. Checklist Dataset <https://doi.org/10.15468/39omei> accessed via GBIF.org on 2018-05-22.
- Geib JC, Strange JP, Galen C (2014) Bumble bee nest abundance, foraging distance, and host plant reproduction: implications for management and conservation. *Ecol Applic* 25:768-778
- GeneMapper Software version 4.0 Applied Biosystems 2009.
- Gezon ZJ, Wyman ES, Ascher JS, Inouye DW, Irwin RE (2015) The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods Ecol Evol* 6:1044-1054
- Goldstein DB, Roemer GW, Smith DA, Reich DE, Bergman A, Wayne RK (1997) The use of microsatellite variation to infer population structure and demographic history in a natural model system. *Genetics* 151:797-801
- Goudet J (2002) FSTAT, A program to estimate and test gene diversities and fixation indices, version 2.9.3. ed. Laussane: UNIL

- Goulson D, Lye GC, Darvill B (2008) The Decline and Conservation of Bumble bees. *Ann Rev Ent* 53:191-208
- Goulson D (2010) Bumble bees: behavior, ecology, and conservation. New York: Oxford University Press. Print.
- Goulson D, Kaden JC, Lepais O, Lye GC, Darvill B (2011) Population structure, dispersal and colonization history of the garden bumble bee *Bombus hortorum* in the Western Isles of Scotland. *Con Gen* 12:867-879
- Goulson D, Nicholls E (2016) The canary in the coalmine; bee declines as an indicator of environmental health. *Sci Prog* 99:312-326
- Goverde M, Schwiezer K, Baur B, Erhardt A (2002) Small-scale habitat fragmentation effects on pollinator behavior: experimental evidence from the bumble bee *Bombus veteranus* on calcareous grasslands. *Biol Conserv* 104:293-299
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* DOI 10.1007/s00442-007-0752-9
- Hadley AS, Betts MG (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biol Rev* 87:526-544
- Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol J Linnean Soc* 42:3-16
- Hawkes C (2009) Linking movement behavior, dispersal and population processes: is individual variation key? *J of Anim Ecol* 78(5): 894- 906

Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution* 59: 1633-1638

Hegland SJ, Nielsen A, Lazaro A, Bjerknes AL, Totland O (2009) How does climate warming affect plant-pollinator interactions? *Ecol Lett* 12(2): 184-195

Heinrich B (1976) The resource specializations of individual bumble bees. *Ecol Mon* 46:105-128

Heinrich B (1979) Resource heterogeneity and patterns of movement in foraging bumble bees. 40:235-245

Herrera JM, Ploquin EF, Rodrigues-Perez J, Obeso JR (2014) Determining habitat suitability for bumble bees in a mountain system: a baseline approach for testing the impact of climate change on the occurrence and abundance of species. *J Biogeogr* 41:700-712

Hijmans R, Cameron SE, Parra JL, Jarvis A, et al. (2005) Very high resolution interpolated climate surfaces of global land areas. *Intl J Climatology* 25:1965-1978

Hijmans RJ, Elith J (2017) Species distribution modeling with R.

Hingston AB (2006) Is the exotic bumble bee *Bombus terrestris* really invading Tasmanian native vegetation? *J Ins Cons* 10:289-293

Hingston AB, Marsden-Smedley J, Driscoll DA (2002) Extent of invasion of Tasmanian native vegetation by the exotic bumble bee *Bombus terrestris* (Apoidea: Apidae). *Australian Ecology* 27:162–17

Holbrook JD, Arkle RS, Rachlow JL, Vierling KT, Pilliod DS (2015) Sampling animal sign in heterogeneous environments: How much is enough? *J Arid Env* 119:51-55

- Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K (2015) Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Phot Eng and Rem Sens* 81(5):345-354
- Hopkins I (1914) History of the bumble bee in New Zealand: its introduction and results. *New Zealand Department of Agriculture, Industry and Commerce* 46:1-29
- Invitrogen® PureLink Genomic DNA Mini Kit (2012) Life Technologies Corporation. Carlsbad, CA.
- Iserbyt S, Vray S, Dendoncker N, Viart S, Rasmont P (2016) High-resolution distribution of bumble bees (*Bombus* spp.) in a mountain area marked by agricultural decline. *Annales de la Société entomologique de France* doi: 10.1080/00379271.2016.1141664
- Jha S (2015) Contemporary human-altered landscapes and oceanic barriers reduce bumble bee gene flow. *Mol Ecol* 24: 993- 1006
- Jha S, Kremen C (2013) Urban land use limits regional bumble bee gene flow. *Mol Ecol* 22:2483-2495
- Jones OR, Wang J (2009) COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol Ecol Res* 10:551-555
- Jost L (2008) GST and its relatives do not measure differentiation. *Mol Ecol* 17:4015-4026

- Kearns CA, Thomson JD (2001) The Natural History of Bumble bees A Sourcebook for Investigations. University Press of Colorado, Boulder, Colorado.
- Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweigher O, Colla SR, Richardson LL, Wagner DL, Gall LF, Sikes DS, Pantoja A (2015) Climate change impacts on bumble bees converge across continents. *Science* 349:177-180
- Kie JG, Bowyer RT, Nicholson MC, Loft ER, et al. (2002) Landscape Heterogeneity at Differing Scales: Effects on Spatial Distribution of Mule Deer. *Ecology* 83(2): 530-544
- Knight ME (2009) Bumble bee nest density and the scale of available forage in arable landscapes. *Insect Cons Div* 2:116-124
- Koch J, Strange J, Williams P (2012) Bumble Bees of the Western United States. US Forest Service Department of Agriculture and the Pollinator Partnership.
- Koch JB, Looney C, Sheppard WS, Strange JP (2017) Patterns of population genetic structure and diversity across bumble bee communities in the Pacific Northwest. *Cons Gen* 18:507-520
- Kraus FB, Wolf S, Moritz RFA (2009) Male flight distance and population substructure in the bumblebee *Bombus terrestris*. *J Animal Ecol* 78: 247-252
- Kudo G (2013) Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecol Res* 29:571-581

- Legendre P, Legendre L (1998) Numerical Ecology, Volume 24, 2nd edition. Elsevier Science.
- Lepais O, Darvill B, O'Connor S, Goulson D (2010) Estimation of bumblebee queen dispersal using sibship reconstruction method. *Mol Ecol* 19(4): 819-31
- Lozier JD, Strange JP, Koch JB (2013) Landscape heterogeneity predicts gene flow in a widespread polymorphic bumble bee, *Bombus bifarius* (Hymenoptera: Apidae). *Cons Gen* 14:1099-1110
- Lozier JD, Strange JP, Stewart IJ, Cameron SA (2011) Patterns of range-wide genetic variation in six North American bumble bee (Apidae: *Bombus*) species. *Mol Ecol* 23:4870-4888
- Lozier JD, Strange JP, Koch JB (2013) Landscape heterogeneity predicts gene flow in a widespread polymorphic bumble bee, *Bombus bifarius* (Hymenoptera: Apidae). *Cons Gen* 14:1099-1110
- Lozier JD, Jackson JM, Dillon ME, Strange JP (2015) Population genomics of divergence among extreme and intermediate color forms in a polymorphic insect. *Ecol Evol Biol* 4:1075-1091
- Manino A, Patetta A, Poporato M, Quaranta M, Intoppa F, Piazza MG, Frilli F (2007) Bumble bee (*Bombus Latrielle*, 1802) Distribution in High Mountains and Global Warming. *Redia*, XC 125-129
- Martin KA (2001) Wildlife in Alpine and Sub-alpine Habitats. *Wildlife-Habitat Relationships in Oregon and Washington*. Oregon State University Press: 285- 310

- Martins AC, De Paiva SD, Melo GAR, De Marco P (2015) Species conservation under future climate change: the case of *Bombus bellicosus*, a potentially threatened South American bumble bee species. *J Insect Cons* 19:33-43
- McDonald K, Brown J H (1992) Using Montane Mammals to Model Extinctions Due to Global Change. *Cons Biol* 6:409- 415
- McRae BH, VB Shah, A Edelman (2006) Circuitscape: Modeling Landscape Connectivity to Promote Conservation and Human Health. The Nature Conservancy, Collins, CO.
- Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36: 1058 1069
- Miller-Rushing AJ, Inouye DW (2009) Variation in the Impact of Climate Change on Flowering Phenology and Abundance: An Examination of Two Pairs of Closely Related Wildflower Species. *Amer J Botany* 96(10):1821-1829
- Miller-Struttmann NE, Geib JC, Franklin JD, Kevan PG, Holdo RM, Ebert-May D, Lynn AM, Kettenbach JA, Hedrick E, Galen C (2015) Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* 349:1541-1544
- Naimi B (2017) R package 'usdm'. Uncertainty Analysis for Species Distribution Models.
- Nei M (1973) Analysis of gene diversity in subdivided populations. *PNAS* 70:3321–3323.
- Nei M (1975) *Molecular Population Genetics and Evolution*. North-Holland Publishing Co., Amsterdam, The Netherlands.
- Nei M (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York.

- Nei M, Chesser R (1983) Estimation of fixation indexes and gene diversities. *Annals of Human Genetics* 47:253-259.
- Osborne JL, Clark SJ, Morris RJ, Williams IH, Riley JR, Smith AD, Reynolds DR, Edwards AS (1999) A landscape study of bumble bee foraging range and constancy, using harmonic radar. *J Applied Ecol* 36:519-533
- Osborne JL, Martin AP, Carreck NL, Swain JL, Knight ME, Goulson D, Hale RJ, Sanderson RA (2008) Bumble bee flight distances in relation to the forage landscape. *J Animal Ecol* 77:406-415
- Penado A, Rebelo H, Goulson D (2016) Spatial distribution modeling reveals climatically suitable areas for bumblebees in undersampled parts of the Iberian Peninsula. *Ins Conserv and Div* 9: 391- 401
- Persson AS, Smith HG (2013) Seasonal persistence of bumble bee populations is affected by landscape context. *Agri, Ecol, and Environ* 165:201-209
- Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol App* 19(1): 181-197
- Pirounakis K, Koulianos S, Schmid-Hempel P (1998) Genetic variation among European populations of *Bombus pascuorum* (Hymenoptera: Apidae) using mitochondrial DNA sequence data. *Euro J Entomol* 95:27-33
- Pompanon F, Bonin A, Taberlet P (2005) Genotyping errors: causes, consequences and resolutions. *Nat Rev: Genetics* 6:847-859

- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959
- Pyke GH (1978) Optimal body size in bumble bees. *Oecologia* 34:255-266
- Pyke GH, Inouye DW, Thomson JD (2011) Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. *Ecol Entomol* 36:511-521
- Pyke GH, Inouye DW, Thomson JD (2012) Local Geographic Distributions of Bumble Bees Near Crested Butte, Colorado: Competition and Community Structure Revisited. *Environ Ent* 41:1332–1349
- Rasmont P (1983) Catalogue of the bumble bees of the west Palearctic region. *Notes faunique de Gembloux* 7:71
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J Heredity* 86:248-249
- Richards CM, Church S, McCauley DE (1999) The Influence of Population Size and Isolation on Gene Flow by Pollen in *Silene alba*. *Evolution* 53:66-73
- Rimmer, L (2015) Thesis: Recovery of an alpine *Bombus* community following drought mediated population contractions. Appalachian State University, North Carolina
- Rocky Mountain National Park Continental Divide Research Learning Center (RMNP) (2007) Climate Change in Rocky Mountain National Park: Preservation in the Face of Uncertainty. National Park Service, US Department of the Interior.

- Rousset F (2008) Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Mol Ecol* 8:103-106
- Rousset F, Lopez J, Belkhir K (2017) Population Genetic Data Analyses Using Genepop. R package 'genepop'.
- Rundel PW, Millar CI (2016) US Forest Service. Alpine ecosystems. In: Zavaleta E, Mooney H, eds. *Ecosystems of California*. Berkeley, California: University of California Press (29):613-634
- Saville NM (1993) Bumble bee ecology in woodlands and arable farmland. Ph.D. Thesis, University of Cambridge.
- Schaffer M, Wratten SD (1994) Bumble bee (*Bombus terrestris*) movement in an intensive farm landscape. In: *Proceedings of the 47th New Zealand Plant Protection Conference*: 253-256. New Zealand Plant Protection Society, Rotorua, New Zealand.
- Schmid-Hempel R, Eckhardt M, Goulson D (2014) The invasion of southern South America by imported bumble bees and associated parasites. *J Animal Ecol* 83:823-837
- Shao ZY, Mao HX, Fu WJ (2004) Genetic structure of Asian populations of *Bombus ignitus* (Hymenoptera: Apidae). *J Heredity* 95:46-52
- Shen G, Yu M, Hu X, Mi X, Ren H, Sun I, Ma K (2009) Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology* 90(11):3033-3041

- Spear SF, Balkenhol N, Fortin MJ, Mcrae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis: Resistance Surfaces in Landscape Genetics. *Mol Ecol* 19:3576–3591
- Thioulouse J, Dray S, Dufour AB, Siberchichot A, Jombart T, Pavoine S (2018) Multivariate Analysis of Ecological Data with ade4.
- Weir BS, Cockerham CC (1984) Estimating F-Statistics for the Analysis of Population Structure. *Evolution* 38(6): 1358-1370
- Widmer A, Schmid-Hempel P, Estoup A, Scholl A (1998) Population genetic structure and colonization history of *Bombus terrestris* (Hymenoptera: apidae) from the Canary Islands and Madeira. *Heredity* 81:563-572
- Widmer A, Schmid-Hempel P (1999) The population genetic structure of a large temperate pollinator species, *Bombus pascuorum* (Scopoli) (Hymenoptera: Apidae). *Mol Ecol* 8:387-398
- Williams PH, Bystriakova N, Huang J, Miao Z, An J (2015) Bumble bees, climate and glaciers across the Tibetan plateau (Apidae: *Bombus* Latrielle). *Systematics and Biodiversity* 13(2):164-181
- Wolf S, Moritz RFA (2008) Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie* 39:419-427
- Wright S (1943a) Isolation by distance. *Genetics* 28: 114

- Wright S (1943b) An analysis of local variability of flower color in *Linanthus parryae*.
Genetics 28: 139
- Wright S (1965) The interpretation of population structure by F-statistics with special regard
to systems of mating. Evolution 19: 395-420
- Xian G, Homer C, Dewitz J, Fry J, Hossain N, Wickham J (2011) The change of impervious
surface area between 2001 and 2006 in the conterminous United States. Phot Eng and
Remote Sensing 77(8):758-762
- Yamamichi M and Innan H (2012) Estimating the migration rate from genetic variation data.
Heredity 108:362-363
- Young N, Carter L, Evangelista P (2011) A MaxEnt Model v. 3.3.3e Tutorial (ArcGIS v 10).
Natural Resource Ecology Laboratory at Colorado State University. Boulder, CO.
- Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement:
a review. Lands Ecol in Review 27:777-797
- Zimmerman ML (1982) Optimal foraging: random movement by pollen collecting bumble
bees. Oecologia 53:394-398

Appendix A: Summer 2017 Field Collections and *Bombus* Floral Preference

Table A1 All *Bombus* individuals collected in summer 2017 in the central Rocky Mountains, Colorado. Location indicates the mountain where individuals were collected. Foraging on indicates whether individuals were caught foraging on a particular flower (noted to genus and species when possible) or caught on the fly. For caste, *Q* indicates queen, *W* indicates worker, *M* indicates male

ID	Species	Location	Elevation	GPS Coordinates	Foraging on	Caste
1	Sylvicola	Democrat	3823	39.33721N 106.12581W	Trifolium perryi	Q
2	Bifarius	Democrat	3823	39.33721N 106.12581W	Penstemon grandiflorus	Q
3	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
4	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
5	Balteatus?	Democrat	3823	39.33721N 106.12581W	Mertensia	W
6	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
7	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
8	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
9	Frigidus	Democrat	3823	39.33721N 106.12581W	Salix	W
10	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
11	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
12	Sylvicola	Democrat	3823	39.33721N 106.12581W	Mertensia	Q
13	Balteatus	Democrat	3823	39.33721N 106.12581W	Mertensia	W
14	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
15	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
16	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
17	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
18	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
19	Bifarius	Democrat	3823	39.33721N 106.12581W	Salix	Q
20	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
21	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
22	?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
23	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
24	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
25	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
26	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
27	?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q

28	Flavifrons	Democrat	3823	39.33721N 106.12581W	On the wing	Q
29	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
30	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
31	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	Q
32	Balteatus	Democrat	3823	39.33721N 106.12581W	Not foraging	Q
33	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
34	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
35	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
36	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
37	Centralis?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	Q
38	Sylvicola	Democrat	3823	39.33721N 106.12581W	Penstemon grandiflorus	W
39	Balteatus	Democrat	3823	39.33721N 106.12581W	Not foraging	W
40	?	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
41	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
42	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
43	Balteatus	Democrat	3823	39.33721N 106.12581W	Mertensia	W
44	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
45	Sylvicola	Democrat	3823	39.33721N 106.12581W	Trifolium perryi	W
46	Balteatus	Democrat	3823	39.33721N 106.12581W	Not foraging	W
47	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
48	Sylvicola	Democrat	3823	39.33721N 106.12581W	Trifolium perryi	W
49	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
50	Sylvicola	Democrat	3823	39.33721N 106.12581W	Penstemon grandiflorus	Q
51	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
52	Balteatus	Democrat	3823	39.33721N 106.12581W	Mertensia	W
53	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
54	Sylvicola	Democrat	3823	39.33721N 106.12581W	Not foraging	Q
55	Sylvicola	Democrat	3823	39.33721N 106.12581W	Trifolium dasyphyllum	W
56	Sylvicola	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
57	Frigidus	Democrat	3823	39.33721N 106.12581W	Salix	Q
58	Sylvicola	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
59	Balteatus	Democrat	3823	39.33721N 106.12581W	Mertensia	W
60	Sylvicola	Democrat	3823	39.33721N 106.12581W	Not foraging	W
61	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
62	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
63	Balteatus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
64	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
65	Frigidus	Democrat	3823	39.33721N 106.12581W	Salix	W
66	Frigidus	Democrat	3823	39.33721N 106.12581W	Castilleja occidentalis	W
67	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
68	Frigidus	Democrat	3823	39.33721N 106.12581W	Salix	W
69	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
70	Sylvicola	Democrat	3823	39.33721N 106.12581W	Salix	W
71	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W

72	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
73	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
74	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Bistort	W
75	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
76	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Aster	W
77	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
78	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Not foraging	W
79	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
80	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Bistort	W
81	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Aster	W
82	Occidentalis	Boreas	3816	39°25.1625 N 105°57.2646 W	SB	W
83	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	N/A	W
84	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
85	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
86	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	W
87	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Polemonium viscosum	W
88	Melanopygus	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium perryi	W
89	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	On the wing	Q
90	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Grass/near nest	W
91	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Castilleja occidentalis	W
92	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Castilleja occidentalis	W
93	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium perryi	W
94	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Bistort	W
95	Sylvicola?	Boreas	3816	39°25.1625 N 105°57.2646 W	N/A	Q
96	Sylvicola?	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	Q
97	Sylvicola?	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	Q
98	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Not foraging	Q
99	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Not foraging	Q
100	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	On the wing	Q
101	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Not foraging	Q
102	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Cruciferacia (Purple Mustard)	Q
103	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Castilleja occidentalis	Q
104	Balteatus	Boreas	3816	39°25.1625 N 105°57.2646 W	Not foraging	Q
105	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Mertensia	Q

106	Sylvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	Q
107	Syvicola	Boreas	3816	39°25.1625 N 105°57.2646 W	Trifolium dasyphyllum	Q
108	Sylvicola	Boreas	3738	39°25.0731 N 105°57.4247 W	Trifolium dasyphyllum	W
109	Balteatus	Boreas	3738	39°25.0731 N 105°57.4247 W	Wing	Q
110	Sylvicola	Boreas	3738	39°25.0731 N 105°57.4247 W	PE	Q
111	Flavifrons	Boreas	3657	39°25.1042 N 105°57.553 W	Yellow Aster	W
112	Frigidus	Boreas	3657	39°25.1042 N 105°57.553 W	Penstemon whippleanus	W
113	Balteatus	Boreas	3657	39°25.1042 N 105°57.553 W	Cirsium (Cirsium clavatum)	W
114	Unknown	Boreas	3657	39°25.1042 N 105°57.553 W	Penstemon whippleanus	W
115	Frigidus	Boreas	3657	39°25.1042 N 105°57.553 W	Unknown yellow star flower	W
116	Balteatus	Boreas	3657	39°25.1042 N 105°57.553 W	Penstemon whippleanus	W
117	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Castilleja occidentalis	W
118	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
119	Balteatus	Boreas	3611	39.42239 N 105.96460 W	WP	W
120	Sylvicola	Boreas	3611	39.42239 N 105.96460 W	Yellow Aster	W
121	Sylvicola	Boreas	3611	39.42239 N 105.96460 W	Big Yellow Aster	W
122	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
123	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Castilleja occidentalis	W
124	Flavifrons	Boreas	3611	39.42239 N 105.96460 W	Penstemon whippleanus	W
125	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Castilleja occidentalis	W
126	Mixtus	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W?
127	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Mertensia	W
128	Flavifrons	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
129	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
130	Flavifrons	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
131	Frigidus	Boreas	3611	39.42239 N 105.96460 W	Big Yellow Aster	W
132	Sylvicola	Boreas	3611	39.42239 N 105.96460 W	Big Yellow Aster	W
133	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
134	Sylvicola	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W
135	Frigidus	Boreas	3611	39.42239 N 105.96460 W	Big Yellow Aster	W
136	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	W
137	Frigidus	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W
138	Frigidus	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W
139	Sylvicola	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W
140	Frigidus	Boreas	3611	39.42239 N 105.96460 W	Small Yellow Aster	W
141	Flavifrons group	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
142	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
143	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
144	Balteatus	Boreas	3786	39.42724 N 105.96384 W	Cirsium (Cirsium clavatum)	W
145	Solitary Bee	Boreas	3786	39.42724 N 105.96384 W	Trifolium dasyphyllum	W
146	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	W
147	Mixtus	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
148	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W

149	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	W
150	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	W
151	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
152	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
153	Flavifrons group	Boreas	3786	39.42724 N 105.96384 W	Penstemon whippleanus	W
154	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
155	Flavifrons group	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	W
156	Frigidus	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	W
157	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
158	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Cirsium (Cirsium clavatum)	W
159	Balteatus	Boreas	3786	39.42724 N 105.96384 W	Cirsium scropularum	W
160	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
161	Sylvicola/Hunti i	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	W
162	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
163	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Tall purple	W
164	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
165	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
166	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
167	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Tall purple	W
168	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Tall purple	W
169	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
170	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
171	Balteatus	Boreas	3562	39.41936 N 105.96338 W	PE	W
172	Balteatus	Boreas	3562	39.41936 N 105.96338 W	Lousewort	W
173	Sylvicola	Boreas	3562	39.41936 N 105.96338 W	White unknown flower	W
174	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
175	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Tall purple	W
176	Flavifrons group	Boreas	3562	39.41936 N 105.96338 W	Mertensia	W
177	Mixtus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
178	Frigidus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
179	Frigidus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
180	Balteatus	Boreas	3513	39.41721 N 105.96591 W	Castilleja occidentalis	W
181	Sylvicola	Boreas	3513	39.41721 N 105.96591 W	Cirsium (Cirsium clavatum)	W
182	Mixtus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
183	Balteatus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
184	Flavifrons group	Boreas	3513	39.41721 N 105.96591 W	Tall pink unknown	W
185	Flavifrons group	Boreas	3513	39.41721 N 105.96591 W	Cirsium (Cirsium clavatum)	W
186	Balteatus	Boreas	3513	39.41721 N 105.96591 W	Tall purple	W
187	Balteatus	Boreas	3513	39.41721 N 105.96591 W	Castilleja occidentalis	W
188	Flavifrons group	Boreas	3513	39.41721 N 105.96591 W	Cirsium (Cirsium clavatum)	W
189	Frigidus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W

190	Mixtus	Boreas	3513	39.41721 N 105.96591 W	Mertensia	W
191	Sylvicola	Boreas	3513	39.41721 N 105.96591 W	Cirsium (Cirsium clavatum)	W
192	Flavifrons group	Boreas	3513	39.41721 N 105.96591 W	Cirsium (Cirsium clavatum)	W
193	Sylvicola	Boreas	3513	39.41721 N 105.96591 W	White unknown flower	W
194	Balteatus	Boreas	3513	39.41721 N 105.96591 W	Castilleja occidentalis	W
195	Flavifrons	Boreas	3562	39.41936 N 105.96338 W	Tall purple	Q
196	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	Q
197	Frigidus	Boreas	3786	39.42724 N 105.96384 W	On the wing	Q
198	Sylvicola	Boreas	3786	39.42724 N 105.96384 W	Big Yellow Aster	Q
199	Syvicola	Boreas	3786	39.42724 N 105.96384 W	Small Yellow Aster	Q
200	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Castilleja occidentalis	Q
201	Balteatus	Boreas	3611	39.42239 N 105.96460 W	Tall purple	Q
202	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8651	Trifolium dasyphyllum	Q
203	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8652	Castilleja occidentalis	Q
204	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8653	Tiny pink	Q
205	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8654	Tiny pink	Q
206	Flavifrons	Horseshoe	4012	39°12.2763 N 106°10.8655	Castilleja occidentalis	Q
207	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8656	Trifolium perryi	Q
208	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8657	Mertensia	Q
209	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8658	Tiny pink	Q
210	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8659	Trifolium perryi	Q
211	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8660	Tiny pink	Q
212	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8661	Tiny pink	Q
213	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8662	Castilleja occidentalis	Q
214	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8663	Castilleja occidentalis	Q
215	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8664	Tiny pink	Q
216	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8665	Tiny pink	W
217	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8666	Tiny pink	W
218	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8667	Small Yellow Aster	W
219	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8668	Trifolium dasyphyllum	W
220	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8669	Tiny white	W
221	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8670	Low egg	W
222	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8671	Mertensia	W
223	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8672	Trifolium perryi	W
224	Sylvicola/Male?	Horseshoe	4012	39°12.2763 N 106°10.8673	Low egg	W
225	Melanopygus	Horseshoe	4012	39°12.2763 N 106°10.8674	Not foraging	W
226	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8675	Trifolium perryi	W
227	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8676	Castilleja occidentalis	W
228	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8677	Low egg	W
229	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8678	Tiny pink	W
230	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8679	Hymenoxys grandiflora	W
231	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8680	Trifolium perryi	W
232	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8681	Mertensia	W
233	Flavifrons	Horseshoe	4012	39°12.2763 N 106°10.8682	N/A	W
234	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8683	Low egg	W

235	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8684	Low egg	W
236	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8685	Not foraging	W
237	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8686	Phacelia (Purple Pincushion)	W
238	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8687	Low egg	W
239	Balteatus	Horseshoe	4012	39°12.2763 N 106°10.8688	Tiny pink	W
240	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8689	Tiny pink	W
241	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8690	Tiny pink	W
242	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8691	Tiny pink	W
243	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8692	Tiny pink	W
244	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8693	Low egg	W
245	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8694	Hymenoxys grandiflora	W
246	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8695	Tiny pink	W
247	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8696	Tiny pink	W
248	Solitary Bee	Horseshoe	4012	39°12.2763 N 106°10.8697	Trifolium dasyphyllum	W
249	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8698	Tiny pink	W
250	Sylvicola	Horseshoe	4012	39°12.2763 N 106°10.8699	Low egg	W
251	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	Q
252	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	Q
253	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	Q
254	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Pink cushion	Q
255	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	Q
256	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	Q
257	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	Q
258	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	Q
259	Flavifrons	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	Q
260	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
261	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
262	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
263	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
264	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
265	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	PE	W
266	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
267	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Small Yellow Aster	W
268	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
269	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Tiny white	W
270	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Low egg	W
271	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
272	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W

273	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
274	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
275	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
276	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
277	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
278	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	W
279	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
280	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
281	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
282	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
283	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
284	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
285	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
286	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W
287	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W
288	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W
289	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
290	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Small Yellow Aster	W
291	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	White Lily	W
292	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W
293	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
294	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
295	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
296	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
297	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
298	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
299	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Tiny pink	W
300	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
301	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
302	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Castilleja occidentalis	W
303	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
304	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
305	Frigidus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
306	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W

307	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Phacelia (Purple Pincushion)	W
308	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Mertensia	W
309	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
310	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium dasyphyllum	W
311	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Bistort	W
312	Balteatus	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Trifolium perryi	W
313	Sylvicola	Horseshoe	3806	39°12.2711 N 106°10.2998 W	Rhodiola rhodantha	W
314	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Big Yellow Aster	W
315	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Trifolium dasyphyllum	W
316	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
317	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
318	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
319	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
320	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Tall purple	W
321	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Tall purple	W
322	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Red Castilleja occidentalis	W
323	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
324	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
325	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
326	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
327	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
328	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
329	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Big Yellow Aster	W
330	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
331	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
332	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
333	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Castilleja occidentalis	W
334	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
335	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
336	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Cirsium scopulorum	W
337	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Castilleja occidentalis	W
338	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Mertensia	W
339	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
340	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W

341	Frigidus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Big Yellow Aster	W
342	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Big Yellow Aster	W
343	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
344	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Big Yellow Aster	W
345	Flavifrons	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
346	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Red Castilleja occidentalis	W
347	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Castilleja occidentalis	W
348	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Castilleja occidentalis	W
349	Balteatus	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Castilleja occidentalis	W
350	Sylvicola	Horseshoe	3642	39°12.3930 N 106°9.8208 W	Penstemon whippleanus	W
351	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	PCastilleja occidentalis	W
352	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Bistort	W
353	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
354	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
355	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Bistort	W
356	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
357	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
358	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
359	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
360	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
361	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
362	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
363	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
364	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
365	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
366	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
367	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
368	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
369	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
370	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Bistort	W
371	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
372	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
373	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
374	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W

375	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Big yellow aster	W
376	Frigidus	Democrat	3708	39°19.8313 N 106°7.5310 W	Big yellow aster	W
377	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Trifolium perryi	W
378	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
379	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
380	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
381	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
382	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
383	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
384	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
385	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
386	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	PCastilleja occidentalis	W
387	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
388	Sylvicola	Democrat	3708	39°19.8313 N 106°7.5310 W	Big yellow aster	W
389	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
390	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	PCastilleja occidentalis	W
391	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
392	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
393	Balteatus	Democrat	3708	39°19.8313 N 106°7.5310 W	Mertensia	W
394	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
395	Flavifrons	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
396	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
397	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
398	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
399	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
400	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Trifolium dasyphyllum	W
401	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Bistort	W
402	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
403	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
404	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
405	Flavifrons	Democrat	3473	39.323757 N 106.12832 W	Cirsium (Cirsium clavatum)	W
406	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
407	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
408	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
409	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
410	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
411	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
412	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Bistort	W
413	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W

414	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
415	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
416	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
417	Frigidus	Democrat	3473	39.323757 N 106.12832 W	Big yellow aster	W
418	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
419	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
420	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
421	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
422	Frigidus	Democrat	3473	39.323757 N 106.12832 W	Rhodiola rhodantha	Q
423	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
424	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
425	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
426	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
427	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
428	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
429	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
430	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
431	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Big yellow aster	W
432	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
433	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
434	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
435	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Mertensia	W
436	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Trifolium perryi	Q
437	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Not foraging	Q
438	Balteatus	Democrat	3473	39.323757 N 106.12832 W	Trifolium dasyphyllum	Q
439	Sylvicola	Democrat	3473	39.323757 N 106.12832 W	Mertensia	Q
440	Centralis	Democrat	3473	39.323757 N 106.12832 W	Mertensia	Q
441	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Rhodiola rhodantha	W
442	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Rhodiola rhodantha	W
443	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
444	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Not foraging	W
445	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
446	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
447	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
448	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
449	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
450	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
451	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
452	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
453	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
454	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
455	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
456	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Mertensia	W
457	Frigidus	Evans	3935	39°36.02 N 105°38.08 W	Rhodiola rhodantha	W
458	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W

459	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
460	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
461	Frigidus	Evans	3935	39°36.02 N 105°38.08 W	Rhodiola rhodantha	W
462	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Moss campion (Tiny Pink)	W
463	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
464	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
465	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
466	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
467	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
468	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
469	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
470	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Hymenoxys grandiflora	W
471	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
473	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
474	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Bistort	W
475	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
476	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Yellow/orange aster	W
477	Balteatus Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
478	(male?)	Evans	3935	39°36.02 N 105°38.08 W	Pedicularis goenlandica	W
479	Balteatus	Evans	3935	39°36.02 N 105°38.08 W	Cirsium scopulorum	W
480	Sylvicola	Evans	3935	39°36.02 N 105°38.08 W	Yellow/orange aster	W
481	Flavifrons	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
482	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
483	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
484	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
485	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
486	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
487	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
488	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
489	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
490	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
491	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
492	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Phacelia (Purple Pincushion)	W
493	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
494	Balteatus	Evans	3889	39.60619 N 105.62687 W	Not foraging	W
495	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
496	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
497	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
498	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
499	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
500	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
501	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
502	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Yellow star (Sedum)	W
503	Frigidus	Evans	3889	39.60619 N 105.62687 W	Yellow star (Sedum)	W
504	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Yellow star (Sedum)	W

505	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Yellow star (Sedum)	W
506	Frigidus	Evans	3889	39.60619 N 105.62687 W	Not foraging	Q
507	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
508	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
509	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
510	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Bistort	W
511	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
512	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
513	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
514	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
515	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
516	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
517	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
518	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
519	Sylvicola	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
520	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
521	Balteatus	Evans	3889	39.60619 N 105.62687 W	Cirsium scopulorum	W
522	Balteatus	Evans	3889	39.60619 N 105.62687 W	Sandwort (Tiny white)	W
523	Melanopygus	Evans	3700	39.63421667 N - 105.6049333 W	White penstemon	W
524	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	N/A	W
525	Melanopygus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
526	Mixtus	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
527	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	White penstemon	W
528	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Yellow (bag in fridge)	W
529	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Phacelia (Purple Pincushion)	W
530	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Phacelia (Purple Pincushion)	W
531	Sylvicola (male)	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
532	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
533	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
534	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Trifolium dasyphyllum	W
535	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Trifolium dasyphyllum	W
536	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
537	Occidentalis?	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
538	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
539	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
540	Melanopygus	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
541	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Trifolium dasyphyllum	W
542	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W

543	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Mertensia	W
544	Mixtus	Evans	3700	39.63421667 N - 105.6049333 W	Phacelia (Purple Pincushion)	W
545	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
546	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
547	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
548	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
549	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
550	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
551	Melanopygus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
552	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
553	Sylvicola?	Evans	3700	39.63421667 N - 105.6049333 W	Pin cushion	W
554	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	White penstemon	W
555	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
556	Centralis	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
557	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
558	Balteatus	Evans	3700	39.63421667 N - 105.6049333 W	Cirsium scopulorum	W
559	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
560	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
561	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
562	Mixtus	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
563	Sylvicola	Evans	3700	39.63421667 N - 105.6049333 W	Bistort	W
564	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	W
565	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
566	Sylvicola	Penn	3964	39.26572 N -106.142 W	Bistort	M
567	Sylvicola	Penn	3964	39.26572 N -106.142 W	Phacelia (Purple Pincushion)	W
568	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
569	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	Q
570	Balteatus	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
571	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
572	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
573	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
574	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	W
575	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
576	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	W
577	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	W
578	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	W
579	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	W
580	Sylvicola	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q

581	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
582	Balteatus	Penn	3964	39.26572 N -106.142 W	Big Yellow Aster	W
583	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	W
584	Sylvicola	Penn	3964	39.26572 N -106.142 W	Small Yellow Aster	M
585	Balteatus	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
586	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	W
587	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M/W ?
588	Centralis	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	W
589	Balteatus	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
590	Balteatus	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
591	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
592	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
593	Sylvicola	Penn	3964	39.26572 N -106.142 W	Big Yellow Aster	M
594	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
595	Balteatus	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
596	Sylvicola	Penn	3964	39.26572 N -106.142 W	Yellow aster	M
597	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	W
598	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
599	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
600	Sylvicola	Penn	3964	39.26572 N -106.142 W	Penstemon whippleanus	Q
601	Sylvicola	Penn	3964	39.26572 N -106.142 W	Trifolium dasyphyllum	W
602	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
603	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
604	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
605	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
606	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
607	Balteatus	Penn	3964	39.26572 N -106.142 W	Polemonium viscosum	Q
608	Balteatus	Penn	3964	39.26572 N -106.142 W	Castilleja occidentalis	Q
609	Flavifrons	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	Q
610	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
611	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
612	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
613	Frigidus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
614	Melanopygus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
615	Melanopygus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
616	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
617	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
618	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
619	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
620	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	M
621	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
622	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
623	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
624	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
625	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W

626	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Phacelia (Purple Pincushion)	W
627	Frigidus	Penn	3757	39.25501 N 106.12684 W	Phacelia (Purple Pincushion)	W
628	Mixtus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
629	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
630	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
631	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
632	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
633	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
634	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
635	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
636	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
637	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
638	Frigidus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
639	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
640	Frigidus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
641	Sylvicola	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
642	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
643	Frigidus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
644	Frigidus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
645	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
646	Balteatus	Penn	3757	39.25501 N 106.12684 W	Penstemon whippleanus	W
647	*	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
648	Frigidus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
649	Frigidus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
650	Frigidus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
651	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
652	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
653	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
654	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
655	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
656	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
657	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
658	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
659	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
660	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
661	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Cirsium clavatum	W
662	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Cirsium clavatum	W
663	Balteatus	Penn	3650	39.25224 N 106.11995 W	RCastilleja occidentalis	Q
664	Balteatus	Penn	3650	39.25224 N 106.11995 W	RCastilleja occidentalis	Q
665	Balteatus	Penn	3650	39.25224 N 106.11995 W	RCastilleja occidentalis	Q
666	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
667	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
668	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Senicio	W
669	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
670	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W

671	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
672	Flavifrons	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
673	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	Q
674	Appositus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
675	Frigidus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
676	Balteatus	Penn	3650	39.25224 N 106.11995 W	Castilleja occidentalis	W
677	Balteatus	Penn	3650	39.25224 N 106.11995 W	Cirsium clavatum	W
678	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Senicio	W
679	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
680	Balteatus	Penn	3650	39.25224 N 106.11995 W	Castilleja occidentalis	W
681	Balteatus	Penn	3650	39.25224 N 106.11995 W	Castilleja occidentalis	W
682	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Purple aster	W
683	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Big Yellow Aster	W
684	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Big Yellow Aster	W
685	Balteatus	Penn	3650	39.25224 N 106.11995 W	Castilleja occidentalis	W
686	Balteatus	Penn	3650	39.25224 N 106.11995 W	Penstemon whippleanus	W
687	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Not foraging	W
688	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Yellow bag	W
689	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Yellow bag	W
690	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Yellow bag	W
691	Sylvicola	Penn	3650	39.25224 N 106.11995 W	Yellow bag	W
692	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
693	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
694	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
695	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Senicio	W
696	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
697	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
698	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
699	Sylvicola	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
700	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
701	Frigidus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
702	Sylvicola	Penn	3563	39.20702 N 106.16520 W	Yarrow	W
703	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
704	Flavifrons	Penn	3563	39.20702 N 106.16520 W	N/A	W
705	Frigidus	Penn	3563	39.20702 N 106.16520 W	Yarrow	W
706	Sylvicola	Penn	3563	39.20702 N 106.16520 W	Big Yellow Aster	M
707	Frigidus	Penn	3563	39.20702 N 106.16520 W	Yellow aster	W
708	Balteatus	Penn	3563	39.20702 N 106.16520 W	Castilleja occidentalis	W
709	Sylvicola	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
710	Balteatus	Penn	3563	39.20702 N 106.16520 W	Castilleja occidentalis	W
711	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
712	Flavifrons	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
713	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
714	Balteatus	Penn	3563	39.20702 N 106.16520 W	Penstemon whippleanus	W
715	Balteatus	Penn	3563	39.20702 N 106.16520 W	Castilleja occidentalis	Q

716	Frigidus	Penn	3563	39.20702 N 106.16520 W	Aster	W
717	Sylvicola	Penn	3563	39.20702 N 106.16520 W	Cirsium clavatum	M
718	Centralis	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon	W
719	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon	W
720	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
721	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
722	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
723	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
724	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	M
725	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
726	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
727	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
728	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Purple aster	W
729	Flavifrons	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
730	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
731	Flavifrons	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
732	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
733	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
734	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
735	Flavifrons	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
736	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
737	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
738	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
739	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	WPenstemon whippleanus	W
740	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Not foraging	W
741	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon	W
742	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon	W
743	Sylvicola	Quail	3763	39°1.0895 N 106°24.2926 W	Not foraging	W
744	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
745	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
746	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
747	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
748	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
749	Balteatus	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W
750	Flavifrons	Quail	3763	39°1.0895 N 106°24.2926 W	Penstemon whippleanus	W

751	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
752	Occidentalis	Quail	3646	39°0.9016 N 106°24.2499 W	Not foraging	?
753	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Penstemon whippleanus	W
754	Sylvicola?	Quail	3646	39°0.9016 N 106°24.2499 W	Not foraging	W
755	Flavifrons	Quail	3646	39°0.9016 N 106°24.2499 W	Cirsium clavatum	W
756	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
757	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
758	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
759	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Castilleja occidentalis	W
760	Flavifrons	Quail	3646	39°0.9016 N 106°24.2499 W	N/A	W
761	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Penstemon whippleanus	W
762	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Not foraging	M
763	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Purple penstemon	W
764	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Purple penstemon	W
765	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Penstemon whippleanus	W
766	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Tiny white (Sandwort)	W
767	Sylvicola?	Quail	3646	39°0.9016 N 106°24.2499 W	Tiny white (Sandwort)	W
768	Sylvicola?	Quail	3646	39°0.9016 N 106°24.2499 W	Tiny white (Sandwort)	W
769	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Tiny white (Sandwort)	W
770	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Tiny white (Sandwort)	W
771	Flavifrons	Quail	3646	39°0.9016 N 106°24.2499 W	Penstemon whippleanus	W
772	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Castilleja occidentalis	W
773	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
774	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
775	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
776	Balteatus	Quail	3646	39°0.9016 N 106°24.2499 W	Purple penstemon	W
777	Melanopygus	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
778	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
779	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
780	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
781	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
782	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
783	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W
784	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Big Yellow Aster	W

785	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Small Yellow Aster	W
786	Rufocinctus	Quail	3646	39°0.9016 N 106°24.2499 W	Trifolium dasyphyllum	W
787	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Sandwort (Fenders)	W
788	Sylvicola	Quail	3646	39°0.9016 N 106°24.2499 W	Sandwort (Fenders)	W
789	Mixtus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
790	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
791	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
792	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
793	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
794	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
795	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
796	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
797	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
798	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	M
799	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
800	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
801	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
802	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
803	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
804	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
805	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
806	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
807	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
808	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
809	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	Q
810	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	N/A	Q
811	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
812	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
813	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
814	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	N/A	W
815	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
816	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
817	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
818	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W

819	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
820	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
821	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
822	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Castilleja occidentalis	W
823	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
824	Sylvicola	Quail	3595	39°0.8484 N 106°24.2939 W	Big Yellow Aster	W
825	Balteatus	Quail	3595	39°0.8484 N 106°24.2939 W	Mertensia	W
826	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
827	Flavifrons	Quail	3595	39°0.8484 N 106°24.2939 W	Cirsium clavatum	W
828	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
829	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
830	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
831	Frigidus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
832	Flavifrons	Penn		39.25547 N 106.128 W	Mertensia	W
833	Frigidus	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	W
834	Frigidus	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	W
835	Frigidus	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	W
836	Sylvicola	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	Q
837	Flavifrons	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
838	Sylvicola	Penn		39.25547 N 106.128 W	Senecio	W
839	Sylvicola	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	W
840	Sylvicola	Penn		39.25547 N 106.128 W	Phacelia (Purple Pincushion)	W
841	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
842	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	M
843	Frigidus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
844	Sylvicola	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
845	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
846	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
847	Balteatus	Penn		39.25547 N 106.128 W	Penstemon whippleanus	W
848	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	N/A	M
849	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
850	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
851	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
852	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
853	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
854	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
855	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
856	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Chionophila jaMertensiasoni	W
857	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	M
858	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
859	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Bistort	W
860	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W

861	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
862	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
863	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
864	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
865	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
866	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
867	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
868	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
869	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
870	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
871	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
872	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
873	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
874	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
875	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	M
876	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Mertensia	W
877	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
878	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
879	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	White penstemon	W
880	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
881	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
882	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
883	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
884	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
885	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
886	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
887	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
888	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
889	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Minuardia?	W
890	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
891	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Minuartia?	M
892	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
893	Flavifrons	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
894	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
895	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
896	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	N/A	W
897	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Chionophila jaMertensiasoni	W
898	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Bistort	W
899	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
900	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Mertensia	W
901	Non focal	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
902	Balteatus	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
903	-	Niwot	3600	40.0558333 N -105.5961 W	-	W
904	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W
905	Sylvicola	Niwot	3600	40.0558333 N -105.5961 W	Silene acaulus (Tiny pink)	W

906	Sylvicola	Niwot	3500	40.057156 N -105.589895 W	Minuartia?	W
907	Mixtus	Niwot	3500	40.057156 N -105.589895 W	NA	W
908	Sylvicola	Niwot	3500	40.057156 N -105.589895 W	NA	W
909	Sylvicola	Niwot	3500	40.057156 N -105.589895 W	NA	W
910	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
911	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	M
912	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
913	Balteatus	Niwot	3745	40.05971667 N -105.61645 W	Not foraging	W
914	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
915	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
916	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Silene acaulus (Tiny pink)	W
917	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
918	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	NA	W
919	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
920	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
921	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
922	Balteatus	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
923	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
924	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	NA	W
925	Balteatus	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
926	Balteatus	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
927	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
928	Sylvicola	Niwot	3745	40.05971667 N -105.61645 W	Trifolium dasyphyllum	W
929	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
930	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
931	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
932	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
933	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
934	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
935	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
936	Balteatus	Niwot	3675	40.05731667 N -105.6077833 W	Castilleja occidentalis	W
937	Sylvicola	Niwot	3675	40.05731667 N -105.6077833 W	Sedum	W
938	Frigidus	Niwot	3675	40.05731667 N -105.6077833 W	N/A	W
939	Balteatus	Niwot	3675	40.05731667 N -105.6077833 W	Castilleja occidentalis	W

940	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Gentian	W
941	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
942	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
943	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
944	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
945	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Pedicularis groend.	W
946	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
947	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
948	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
949	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
950	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
951	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
952	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
953	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
954	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
955	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
956	Balteatus	Niwot	3675	40.05731667 N - 105.6077833 W	Castilleja occidentalis	W
957	Sylvicola	Niwot	3675	40.05731667 N - 105.6077833 W	Sedum	W
958	Balteatus	Niwot	35-3600		N/A	W
959	Balteatus	Niwot	35-3600		Chionophila jaMertensiasoni	W
960	Bifarius	Niwot	3745	40.05971667 N -105.61645 W	Sedum	W
102	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	Q
102	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	Q
102	Balteatus	Silverheel	3655	39°20.9870 N 106°1.4520 W	Pink Castilleja occidentalis	Q
102	Occidentalis	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	Q
102	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	On the wing	Q
102	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	Q
103	Balteatus	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	M
103	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	Q
103	Balteatus	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	W
103	Balteatus	Silverheel	3655	39°20.9870 N 106°1.4520 W	Penstemon whippleanus	W
103	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Rhodiola rhodantha	W
103	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Rhodiola rhodantha	W
103	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	Cirsium clavatum	W
103	Sylvicola	Silverheel	3655	39°20.9870 N 106°1.4520 W	White loCastilleja occidentalisweed	W

103		Silverheel		39°20.9870 N 106°1.4520		
8	Sylvicola	s	3655	W	Cirsium clavatum	W
103		Silverheel		39°20.9870 N 106°1.4520		
9	Sylvicola	s	3655	W	Taraxacum officinale	W
104		Silverheel		39°20.9870 N 106°1.4520		
0	N/A?	s	3655	W	Cirsium clavatum	W
104		Silverheel		39°20.9870 N 106°1.4520		
1	Sylvicola	s	3655	W	Cirsium clavatum	W
104		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
104		Silverheel		39°20.9870 N 106°1.4520		
3	Balteatus	s	3655	W	Cirsium clavatum	W
104		Silverheel		39°20.9870 N 106°1.4520		
4	Sylvicola	s	3655	W	Pedicularis goenlandicailla	W
104		Silverheel		39°20.9870 N 106°1.4520		
5	Sylvicola	s	3655	W	Rhodiola rhodantha	W
104		Silverheel		39°20.9870 N 106°1.4520		
6	Sylvicola	s	3655	W	Taraxacum officinale	W
104		Silverheel		39°20.9870 N 106°1.4520	White loCastilleja	
7	Sylvicola	s	3655	W	occidentalisweed	W
104		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Cirsium clavatum	W
104		Silverheel		39°20.9870 N 106°1.4520		
9	Sylvicola	s	3655	W	Penstemon whippleanus	W
105		Silverheel		39°20.9870 N 106°1.4520	White loCastilleja	
0	Sylvicola	s	3655	W	occidentalisweed	W
105		Silverheel		39°20.9870 N 106°1.4520		
1	Sylvicola	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
3	Sylvicola	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
4	Sylvicola	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
5	Sylvicola	s	3655	W	Pedicularis goenlandicailla	W
105		Silverheel		39°20.9870 N 106°1.4520		
6	Flavifrons	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
7	Frigidus	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Cirsium clavatum	W
105		Silverheel		39°20.9870 N 106°1.4520		
9	Sylvicola	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
0	Flavifrons	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
1	Balteatus	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
3	Sylvicola	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
4	Sylvicola	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
5	Flavifrons	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
6	Balteatus	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
7	Sylvicola	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
8	Sylvicola	s	3655	W	Cirsium clavatum	W
106		Silverheel		39°20.9870 N 106°1.4520		
9	Balteatus	s	3655	W	Cirsium clavatum	W
107		Silverheel		39°20.9870 N 106°1.4520		
0	Balteatus	s	3655	W	Cirsium clavatum	W
107		Silverheel		39°20.9870 N 106°1.4520		
1	Balteatus	s	3655	W	Penstemon whippleanus	W

107		Silverheel		39°20.9870 N 106°1.4520		
2	Flavifrons	s	3655	W	Penstemon whippleanus	W
107		Silverheel		39°20.9870 N 106°1.4520		
3	Balteatus	s	3655	W	Penstemon whippleanus	W
107		Silverheel		39°20.9870 N 106°1.4520		
4	Balteatus	s	3655	W	Purple Castilleja occidentalis	W
107		Silverheel		39°20.9870 N 106°1.4520		
5	Sylvicola	s	3655	W	Kings crown	W
107		Silverheel		39°20.9870 N 106°1.4520		
6	Sylvicola	s	3655	W	On the wing	W
107		Silverheel		39°20.9870 N 106°1.4520		
7	Balteatus	s	3655	W	Cirsium clavatum	W
107		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Penstemon whippleanus	W
107		Silverheel		39°20.9870 N 106°1.4520		
9	Balteatus	s	3655	W	Cirsium clavatum	W
108		Silverheel		39°20.9870 N 106°1.4520		
0	Sylvicola	s	3655	W	Cirsium clavatum	W
108		Silverheel		39°20.9870 N 106°1.4520		
1	Sylvicola	s	3655	W	N/A	W
108		Silverheel		39°20.0073 N 106°2.3609		
2	Balteatus	s	3630	W	Purple (fridge)	W
108		Silverheel		39°20.0073 N 106°2.3609		
3	Sylvicola	s	3630	W	Small yellow aster	M
108		Silverheel		39°20.0073 N 106°2.3609		
4	Sylvicola	s	3630	W	Small yellow aster	M
108		Silverheel		39°20.0073 N 106°2.3609		
5	Sylvicola	s	3630	W	Yellow aster	W
108		Silverheel		39°20.0073 N 106°2.3609		
6	Frigidus	s	3630	W	Potentilla	W
108		Silverheel		39°20.0073 N 106°2.3609		
7	Sylvicola	s	3630	W	Small yellow aster	W
108		Silverheel		39°20.0073 N 106°2.3609		
8	Sylvicola	s	3630	W	On the wing	W
108		Silverheel		39°20.0073 N 106°2.3609		
9	Sylvicola	s	3630	W	Yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
0	Sylvicola	s	3630	W	Small yellow aster	M
109		Silverheel		39°20.0073 N 106°2.3609		
1	Sylvicola	s	3630	W	Small yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
2	Sylvicola	s	3630	W	Small yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
3	Balteatus	s	3630	W	Yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
4	Sylvicola	s	3630	W	Small yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
5	Sylvicola	s	3630	W	Yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
6	Sylvicola	s	3630	W	Small yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
7	Sylvicola	s	3630	W	Yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
8	Sylvicola	s	3630	W	Small yellow aster	W
109		Silverheel		39°20.0073 N 106°2.3609		
9	Centralis	s	3630	W	Mertensia	W
110		Silverheel		39°20.0073 N 106°2.3609		
0	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
1	Sylvicola	s	3630	W	Small yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
2	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
3	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
4	Sylvicola	s	3630	W	Small yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
5	Balteatus	s	3630	W	Small yellow aster	W

110		Silverheel		39°20.0073 N 106°2.3609		
6	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
7	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
8	Sylvicola	s	3630	W	Yellow aster	W
110		Silverheel		39°20.0073 N 106°2.3609		
9	Sylvicola	s	3630	W	Yellow aster	W
111		Silverheel		39°20.0073 N 106°2.3609		
0	Balteatus	s	3630	W	Purple (fridge)	W
111		Silverheel		39°20.0073 N 106°2.3609		
1	Balteatus	s	3630	W	Purple (fridge)	W
111		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
3	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
4	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
5	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
6	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
7	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Cirsium clavatum	W
111		Silverheel		39°20.9870 N 106°1.4520		
9	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
0	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
1	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	M
112		Silverheel		39°20.9870 N 106°1.4520		
3	Balteatus	s	3655	W	Cirsium clavatum	M
112		Silverheel		39°20.9870 N 106°1.4520		
4	Balteatus	s	3655	W	Cirsium clavatum	M
112		Silverheel		39°20.9870 N 106°1.4520		
5	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
6	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
7	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Cirsium clavatum	W
112		Silverheel		39°20.9870 N 106°1.4520		
9	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
0	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
1	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
3	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
4	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
5	Flavifrons	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
6	Balteatus	s	3655	W	On the wing	W
113		Silverheel		39°20.9870 N 106°1.4520		
7	Flavifrons	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
8	Balteatus	s	3655	W	Cirsium clavatum	W
113		Silverheel		39°20.9870 N 106°1.4520		
9	Balteatus	s	3655	W	Cirsium clavatum	W

114		Silverheel		39°20.9870 N 106°1.4520		
0	Balteatus	s	3655	W	Cirsium clavatum	W
114		Silverheel		39°20.9870 N 106°1.4520		
1	Flavifrons	s	3655	W	Cirsium clavatum	W
114		Silverheel		39°20.9870 N 106°1.4520		
2	Balteatus	s	3655	W	Cirsium clavatum	W
114						
3	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Small yellow aster	M
114						
4	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Bistort	M
114						
5	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Small yellow aster	M
114						
6	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Bistort	M
114						
7	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Unknown white	W
114						
8	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Yellow aster	W
114						
9	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Yellow aster	W
115						
0	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
115						
1	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
115						
2	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	M
115						
3	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
115						
4	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
115						
5	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
115						
6	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
115						
7	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
115						
8	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
115						
9	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Speedwell	W
116						
0	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	On the wing	W
116						
1	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Unknown purple	W
116						
2	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
3	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
4	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
5	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
6	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
7	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
116						
8	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
116						
9	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
117						
0	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Penstemon whippleanus	W
117						
1	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Little white?	W
117						
2	Melanopygus	Elbert	3770	39°7.7661 N 106°25.614 W	Big Yellow Aster	W
117						
3	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W

117						
4	Mixtus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
117						
5	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
117						
6	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
117						
7	Unknown	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
117						
8	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
117						
9	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Sandwort (Fenders)	W
118						
0	Centralis	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
1	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
2	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
3	Mixtus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
4	Mixtus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
5	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
118						
6	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Purple aster	W
118						
7	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Small yellow aster	W
118						
8	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Small yellow aster	W
118						
9	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Small yellow aster	W
119						
0	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
1	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
2	Flavifrons	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
3	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
4	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
5	Balteatus	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
6	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
7	Sylvicola	Elbert	3770	39°7.7661 N 106°25.614 W	Mertensia	W
119						
8	Flavifrons	Elbert	3681	39°7.8340 N 106°25.4733 W	Cirsium clavatum	W
119						
9	Flavifrons	Elbert	3681	39°7.8340 N 106°25.4733 W	Cirsium clavatum	W
120						
0	Balteatus	Elbert	3681	39°7.8340 N 106°25.4733 W	Castilleja occidentalis	W
120						
1	Melanopygus	Elbert	3681	39°7.8340 N 106°25.4733 W	Sandwort (Fenders)	W
120						
2	Sylvicola	Elbert	3681	39°7.8340 N 106°25.4733 W	Sandwort (Fenders)	W
120						
3	Melanopygus	Elbert	3681	39°7.8340 N 106°25.4733 W	Sandwort (Fenders)	W
120						
4	Mixtus	Elbert	3681	39°7.8340 N 106°25.4733 W	Sandwort (Fenders)	W
120						
5	Mixtus	Elbert	3681	39°7.8340 N 106°25.4733 W	TWS	W
120						
6	Mixtus	Elbert	3681	39°7.8340 N 106°25.4733 W	TWS	W
120						
7	Sylvicola	Elbert	3681	39°7.8340 N 106°25.4733 W	TWS	W

120				39°7.8340 N 106°25.4733		
8	Sylvicola	Elbert	3681	W	TWS	W
120				39°7.8340 N 106°25.4733		
9	Melanopygus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
0	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
121				39°7.8340 N 106°25.4733		
1	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
121				39°7.8340 N 106°25.4733		
2	Frigidus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
3	Sylvicola	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
4	Mixtus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
5	Mixtus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
6	Melanopygus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
7	Mixtus	Elbert	3681	W	TWS	W
121				39°7.8340 N 106°25.4733		
8	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
121				39°7.8340 N 106°25.4733		
9	Mixtus	Elbert	3681	W	Sandwort (Fenders)	W
122				39°7.8340 N 106°25.4733		
0	Melanopygus	Elbert	3681	W	Penstemon whippleanus	W
122				39°7.8340 N 106°25.4733		
1	Flavifrons	Elbert	3681	W	Penstemon whippleanus	W
122				39°7.8340 N 106°25.4733		
2	Frigidus	Elbert	3681	W	Sandwort (Fenders)	W
122				39°7.8340 N 106°25.4733		
3	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
122				39°7.8340 N 106°25.4733		
4	Mixtus	Elbert	3681	W	Sandwort (Fenders)	W
122				39°7.8340 N 106°25.4733		
5	Balteatus	Elbert	3681	W	Castilleja occidentalis	W
122				39°7.8340 N 106°25.4733		
6	Flavifrons	Elbert	3681	W	Castilleja occidentalis	W
122				39°7.8340 N 106°25.4733		
7	Sylvicola	Elbert	3681	W	Yellow aster	W
122				39°7.8340 N 106°25.4733		
8	Frigidus	Elbert	3681	W	Yellow aster	W
122				39°7.8340 N 106°25.4733		
9	Frigidus	Elbert	3681	W	Yellow aster	M
123				39°7.8340 N 106°25.4733		
0	Frigidus	Elbert	3681	W	Yellow aster	W
123				39°7.8340 N 106°25.4733		
1	Frigidus	Elbert	3681	W	Sandwort (Fenders)	W
123				39°7.8340 N 106°25.4733		
2	Frigidus	Elbert	3681	W	Sandwort (Fenders)	W
123				39°7.8340 N 106°25.4733		
3	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
123				39°7.8340 N 106°25.4733		
4	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
123				39°7.8340 N 106°25.4733		
5	Frigidus	Elbert	3681	W	Small yellow aster	W
123				39°7.8340 N 106°25.4733		
6	Sylvicola	Elbert	3681	W	Small yellow aster	W
123				39°7.8340 N 106°25.4733		
7	Appositus?	Elbert	3681	W	Small yellow aster	W
123				39°7.8340 N 106°25.4733		
8	Flavifrons	Elbert	3681	W	Sandwort (Fenders)	W
123				39°7.8340 N 106°25.4733		
9	Balteatus	Elbert	3681	W	Sandwort (Fenders)	W
124				39°7.8340 N 106°25.4733		
0	Flavifrons	Elbert	3681	W	Sandwort (Fenders)	W
124				39°7.8340 N 106°25.4733		
1	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W

124				39°7.8340 N 106°25.4733		
2	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
124				39°7.8340 N 106°25.4733		
3	Flavifrons	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
4	Sylvicola	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
5	Mixtus	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
6	Sylvicola	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
7	Sylvicola	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
8	Sylvicola	Elbert	3681	W	Small yellow aster	W
124				39°7.8340 N 106°25.4733		
9	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
0	Unknown	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
1	Flavifrons	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
2	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
3	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
4	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
5	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W
125				39°7.8340 N 106°25.4733		
6	Flavifrons	Elbert	3681	W	Yellow aster	W
125				39°7.8340 N 106°25.4733		
7	Sylvicola	Elbert	3681	W	Yellow aster	W
125				39°7.8340 N 106°25.4733		
8	Flavifrons	Elbert	3681	W	Yellow aster	W
125				39°7.8340 N 106°25.4733		
9	Sylvicola	Elbert	3681	W	Yellow aster	W
126				39°7.8340 N 106°25.4733		
0	Sylvicola	Elbert	3681	W	Yellow aster	W
126				39°7.8340 N 106°25.4733		
1	Frigidus	Elbert	3681	W	Yellow aster	W
126				39°7.8340 N 106°25.4733		
2	Sylvicola	Elbert	3681	W	Sandwort (Fenders)	W

Appendix B: Supplementary Tables and Figures

Table A2 Total number of specimens collected from each elevation within each site

Site	Elevation (m)	Number of Specimens	Total
Boreas	3513	5	41
	3562	8	
	3611	12	
	3657	2	
	3738	1	
	3786	2	
	3816	11	
Democrat	3473	32	96
	3708	36	
	3823	28	
Elbert	3681	3	16
	3770	13	
Evans	3700	13	51
	3889	27	
	3935	11	
Horseshoe	3642	19	55
	3806	28	
	4012	8	
Niwot	3600	28	45
	3675	13	
	3745	4	
Penn	3563	10	48
	3650	9	
	3757	12	
	3964	17	
Quail	3595	17	41
	3646	8	
	3763	16	
Silverheels	3630	5	52
	3655	48	
Total			446

Table A3 Tests for Hardy-Weinberg probability and heterozygote deficiency by locus and population. Significant values are in bold and standard error is reported

Locus	Population	Probability test		Heterozygote deficiency		Heterozygote excess	
		P-value	SE	P-value	SE	P-value	SE
B124	Democrat	0.0788	0.0198	0.0145	0.0060	0.9855	0.0060
	Boreas	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Horseshoe	0.0426	0.0074	0.0105	0.0039	0.9897	0.0039
	Evans	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Penn	0.1321	0.0243	0.2489	0.0304	0.7539	0.0301
	Quail	0.3243	0.0271	0.0018	0.0010	0.9995	0.0005
	Niwot	0.3597	0.0271	0.7149	0.0231	0.2938	0.0237
	Silverheels	0.0520	0.0145	0.1532	0.0261	0.8519	0.0253
	Elbert	0.0198	0.0093	0.0116	0.0053	0.9905	0.0044
BTERN01	Democrat	0.4262	0.0298	0.0310	0.0082	0.9690	0.0082
	Boreas	0.9137	0.0123	0.4210	0.0296	0.5836	0.0296
	Horseshoe	0.1781	0.0279	0.0527	0.0147	0.9473	0.0147
	Evans	0.0136	0.0076	0.0000	0.0000	1.0000	0.0000
	Penn	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Quail	0.1189	0.0191	0.0658	0.0147	0.9343	0.0147
	Niwot	0.2819	0.0323	0.0242	0.0077	0.9758	0.0077
	Silverheels	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Elbert	0.0260	0.0094	0.0012	0.0012	1.0000	0.0000
BT10	Democrat	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Boreas	0.0514	0.0139	0.0066	0.0058	0.9934	0.0058
	Horseshoe	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Evans	0.5066	0.0277	0.3040	0.0279	0.6998	0.0281
	Penn	0.0011	0.0011	0.0014	0.0011	0.9986	0.0011
	Quail	0.0008	0.0008	0.3219	0.0263	0.6781	0.0263
	Niwot	0.0002	0.0002	0.0192	0.0086	0.9810	0.0086
	Silverheels	0.0002	0.0002	0.0000	0.0000	1.0000	0.0000
	Elbert	0.0122	0.0037	0.0021	0.0013	0.9995	0.0003
BL11	Democrat	0.0444	0.0127	0.0926	0.0117	0.9074	0.0117
	Boreas	0.8415	0.0210	0.2046	0.0277	0.8055	0.0271
	Horseshoe	0.1120	0.0172	0.0000	0.0000	1.0000	0.0000
	Evans	0.0063	0.0054	0.0000	0.0000	1.0000	0.0000
	Penn	0.0019	0.0019	0.0000	0.0000	1.0000	0.0000
	Quail	0.0605	0.0111	0.1078	0.0158	0.8922	0.0158
	Niwot	0.0540	0.0107	0.0045	0.0016	0.9955	0.0016
	Silverheels	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Elbert	0.0027	0.0019	0.0084	0.0056	1.0000	0.0000

BL13	Democrat	0.4030	0.0349	0.0140	0.0057	0.9860	0.0057
	Boreas	0.0818	0.0213	0.4493	0.0379	0.5639	0.0369
	Horseshoe	0.0071	0.0045	0.0504	0.0175	0.9496	0.0175
	Evans	0.2552	0.0282	0.0133	0.0068	0.9867	0.0068
	Penn	0.2413	0.0268	0.8896	0.0215	0.1259	0.0226
	Quail	0.1136	0.0172	0.5905	0.0295	0.4407	0.0298
	Niwot	0.6030	0.0278	0.9586	0.0111	0.0571	0.0121
	Silverheels	0.0179	0.0066	0.0027	0.0018	0.9973	0.0018
	Elbert	0.7646	0.0222	0.2149	0.0254	0.8326	0.0220
B10	Democrat	0.0003	0.0002	0.0000	0.0000	1.0000	0.0000
	Boreas	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
	Horseshoe	0.1697	0.0205	0.0687	0.0119	0.9313	0.0119
	Evans	0.0000	0.0000	0.0009	0.0009	0.9991	0.0009
	Penn	0.0202	0.0086	0.0004	0.0004	0.9996	0.0004
	Quail	0.0125	0.0063	0.0660	0.0144	0.9340	0.0144
	Niwot	0.4953	0.0328	0.5152	0.0350	0.5164	0.0355
	Silverheels	0.0019	0.0019	0.0223	0.0073	0.9778	0.0073
	Elbert	0.5867	0.0137	0.1478	0.0117	0.8569	0.0115
BT28	Democrat	0.2175	-	0.9749	-	0.0703	-
	Boreas	0.5919	-	0.3268	-	0.7964	-
	Horseshoe	1.0000	-	0.7278	-	0.5079	-
	Evans	0.0036	-	0.0034	-	0.9996	-
	Penn	0.6758	-	0.1876	-	0.8849	-
	Quail	1.0000	-	0.4695	-	0.6890	-
	Niwot	1.0000	-	0.6937	-	0.5825	-
	Silverheels	0.0766	-	0.0423	-	0.9925	-
	Elbert	1.0000	-	0.7484	-	0.6481	-
B96	Democrat	0.0379	0.0158	0.1890	0.0339	0.8110	0.0339
	Boreas	0.0142	0.0054	0.0208	0.0115	0.9792	0.0115
	Horseshoe	0.8480	0.0112	0.1973	0.0164	0.8040	0.0161
	Evans	0.2005	0.0315	0.2069	0.0317	0.7932	0.0317
	Penn	0.2855	0.0271	0.7764	0.0244	0.2449	0.0254
	Quail	0.7958	0.0196	0.7586	0.0222	0.2526	0.0230
	Niwot	0.6180	0.0279	0.8711	0.0194	0.1884	0.0236
	Silverheels	0.0312	0.0091	0.3374	0.0350	0.6734	0.0348
	Elbert	0.6910	0.0249	0.5686	0.0327	0.5904	0.0358

Table A4 Log-likelihood ratio and probability tests for LD for each locus pair, across all populations. Significant values are in bold.

Locus Pair	Log-likelihood test			Probability test	
	P-value	Chi ²	df	P-value	Chi ²
B124-BTERN01	0.000000	Infinity	18	0.000000	Infinity
B124-BT10	0.226946	22.114395	18	0.226946	22.114395
BTERN01-BT10	0.660663	15.018991	18	0.660663	15.018991
B124-BL11	0.078409	27.031378	18	0.210784	22.494139
BTERN01-BL11	0.950365	9.376780	18	0.950365	9.376780
BT10-BL11	0.692466	14.551958	18	0.692466	14.551958
B124-BL13	0.134947	22.261514	16	0.134947	22.261514
BTERN01-BL13	0.661124	13.158648	16	0.661124	13.158648
BT10-BL13	0.494793	15.410637	16	0.494793	15.410637
BL11-BL13	0.901077	9.288085	16	0.901077	9.288085
B124-B10	0.000000	Infinity	18	0.000000	Infinity
BTERN01-B10	0.286809	20.854654	18	0.286809	20.854654
BT10-B10	0.015699	33.219283	18	0.019825	32.378144
BL11-B10	0.999549	4.374793	18	0.999585	4.324321
BL13-B10	0.749148	11.924685	16	0.814803	10.913330
B124-BT28	0.761392	13.494628	18	0.725887	14.049070
BTERN01-BT28	0.084705	26.704622	18	0.088995	26.493650
BT10-BT28	0.760711	13.505506	18	0.760185	13.513911
BL11-BT28	0.882903	11.262138	18	0.902299	10.808666
BL13-BT28	0.549748	14.658901	16	0.646473	13.357331
B10-BT28	0.262075	21.351013	18	0.324606	20.146985
B124-B96	0.580749	16.169079	18	0.580749	16.169079
BTERN01-B96	0.974575	8.256139	18	0.974575	8.256139
BT10-B96	0.903930	10.768275	18	0.000000	Infinity
BL11-B96	0.909670	10.622881	18	0.909670	10.622881
BL13-B96	0.563645	14.471325	16	0.563645	14.471325
B10-B96	0.566518	16.373217	18	0.566518	16.373217
BT28-B96	0.228133	22.087282	18	0.295082	20.694937

Table A5 Log likelihood ratio test for linkage disequilibrium for each population and locus pair. Significant values are in bold

Locus Pair	Population								
	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert
B124-BTERN01	0.36896	0.40103	0.06601	0.01051	0.54029	1.00000	1.00000	0.00000	1.00000
B124-BT10	0.00153	0.64058	0.27242	0.67168	1.00000	0.69231	0.69277	0.82770	0.22156
BTERN01-BT10	0.54104	1.00000	0.05756	1.00000	0.45356	0.74314	0.16260	0.32099	1.00000
B124-BL11	0.00474	0.39922	0.52581	0.08337	1.00000	0.37435	0.20491	0.21210	1.00000
BTERN01-BL11	0.34732	0.26690	0.36580	0.46064	1.00000	1.00000	0.58908	1.00000	1.00000
BT10-BL11	0.84040	1.00000	0.10496	0.32127	1.00000	0.62545	0.03904	1.00000	1.00000
B124-BL13	0.01974	1.00000	0.92240	0.00634	0.52475	0.64499	0.90704	0.41351	No info
BTERN01-BL13	0.13394	1.00000	0.75136	0.12445	0.62500	1.00000	1.00000	0.17742	No info
BT10-BL13	0.47245	1.00000	0.08906	0.21431	0.45343	0.79787	1.00000	0.13807	No info
BL11-BL13	0.50224	1.00000	1.00000	0.04294	1.00000	0.44601	1.00000	1.00000	No info
B124-BT10	0.00000	0.45437	0.89431	0.21521	0.68502	0.70350	0.59477	0.10815	1.00000
BTERN01-BT10	0.52620	0.37763	0.20356	0.17998	0.53813	0.07181	0.10526	1.00000	1.00000
BT10-BT10	0.22096	1.00000	0.32870	0.16679	0.10792	0.00841	0.87604	0.08768	0.07243
BL11-BT10	0.83266	1.00000	0.72133	0.55789	1.00000	1.00000	0.99250	0.33740	1.00000
BL13-BT10	0.49791	0.54591	0.08140	0.71456	0.64351	0.80840	0.41428	0.75540	No info
B124-BT28	0.61033	0.78949	0.70289	0.40431	0.39981	0.41716	0.41742	0.84721	0.14536
BTERN01-BT28	0.05753	0.66356	0.01082	0.75352	0.17131	0.23734	0.23045	0.92226	0.59086
BT10-BT28	0.27399	0.64040	0.84672	0.50427	0.2539	0.20545	0.57646	0.51831	1.00000
BL11-BT28	0.77231	0.70634	0.82448	0.81386	0.25487	0.75962	0.08120	0.77237	0.80654
BL13-BT28	0.72984	0.09970	0.04155	0.77845	0.83606	0.56102	0.65340	0.90937	No info
BT10-BT28	0.27986	0.35031	0.02223	0.88699	0.53414	0.36130	0.51374	0.17064	0.70646
B124-B96	0.14818	0.58020	1.00000	0.14289	1.00000	0.08931	1.00000	0.28097	1.00000
BTERN01-B96	0.59870	1.00000	0.23901	1.00000	1.00000	1.00000	1.00000	0.11261	1.00000
BT10-B96	0.07444	1.00000	0.76007	1.00000	0.16336	1.00000	0.49647	1.00000	1.00000
BL11-B96	0.61170	1.00000	0.01322	1.00000	1.00000	1.00000	0.61024	1.00000	1.00000
BL13-B96	0.86785	1.00000	1.00000	0.18926	0.64173	0.33742	0.40408	0.05013	No info
BT10-B96	0.84488	1.00000	0.07824	0.29681	1.00000	0.26587	0.62882	1.00000	0.08486
BT28-B96	0.02079	0.04098	0.78928	0.94152	0.68758	0.24508	0.30253	0.49536	1.00000

Table A6 Probability test for linkage disequilibrium for each population and locus pair.

Significant values are in bold

Locus Pair	Population									
	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert	
B124-BTERN01	0.36896	0.40103	0.06601	0.01051	0.54029	1.00000	1.00000	0.00000	1.00000	
B124-BT10	0.00153	0.64058	0.27242	0.67168	1.00000	0.69231	0.69277	0.82770	0.22156	
BTERN01-BT10	0.54104	1.00000	0.05756	1.00000	0.45356	0.74314	0.16260	0.32099	1.00000	
B124-BL11	0.03995	0.39922	0.52581	0.08337	1.00000	0.37435	0.21363	0.23332	1.00000	
BTERN01-BL11	0.34732	0.26690	0.36580	0.46064	1.00000	1.00000	0.58908	1.00000	1.00000	
BT10-BL11	0.84040	1.00000	0.10496	0.32127	1.00000	0.62545	0.03904	1.00000	1.00000	
B124-BL13	0.01974	1.00000	0.92240	0.00634	0.52475	0.64499	0.90704	0.41351	No Info	
BTERN01-BL13	0.13394	1.00000	0.75136	0.12445	0.62500	1.00000	1.00000	0.17742	No Info	
BT10-BL13	0.47245	1.00000	0.08906	0.21431	0.45343	0.79787	1.00000	0.13807	No Info	
BL11-BL13	0.50224	1.00000	1.00000	0.04294	1.00000	0.44601	1.00000	1.00000	No Info	
B124-BT10	0.00000	0.45437	0.89431	0.25974	0.68502	0.70350	0.53052	0.12546	1.00000	
BTERN01-BT10	0.52620	0.37763	0.20356	0.17998	0.53813	0.07181	0.10526	1.00000	1.00000	
BT10-BT10	0.29967	1.00000	0.32870	0.18728	0.10792	0.00841	0.87604	0.08768	0.07243	
BL11-BT10	0.85394	1.00000	0.72133	0.55789	1.00000	1.00000	0.99250	0.33740	1.00000	
BL13-BT10	0.49791	0.54591	0.13497	0.71456	0.64351	0.80840	0.41428	0.75540	No Info	
B124-BT28	0.50441	0.78949	0.72321	0.36142	0.37878	0.44547	0.39406	0.88443	0.14536	
BTERN01-BT28	0.06254	0.66356	0.01434	0.63752	0.15223	0.24349	0.23045	0.92226	0.59086	
BT10-BT28	0.28019	0.64040	0.85631	0.56818	0.25588	0.18056	0.55619	0.51831	1.00000	
BL11-BT28	0.81288	0.70634	0.82481	0.81459	0.25487	0.75962	0.09539	0.78262	0.80654	
BL13-BT28	0.72022	0.10124	0.06893	0.79509	0.87320	0.56170	0.70409	0.91118	No Info	
BT10-BT28	0.26021	0.35432	0.03351	0.80816	0.52757	0.36925	0.56697	0.21652	0.70646	
B124-B96	0.14818	0.58020	1.00000	0.14289	1.00000	0.08931	1.00000	0.28097	1.00000	
BTERN01-B96	0.59870	1.00000	0.23901	1.00000	1.00000	1.00000	1.00000	0.11261	1.00000	
BT10-B96	0.00000	1.00000	0.76007	1.00000	0.16330	1.00000	0.49647	1.00000	1.00000	
BL11-B96	0.61170	1.00000	0.01322	1.00000	1.00000	1.00000	0.61024	1.00000	1.00000	
BL13-B96	0.86785	1.00000	1.00000	0.18926	0.64173	0.33742	0.40408	0.05013	No Info	
BT10-B96	0.84488	1.00000	0.07824	0.29681	1.00000	0.26587	0.62882	1.00000	0.08486	
BT28-B96	0.03341	0.06123	0.78928	0.94152	0.68758	0.24508	0.24955	0.50172	1.00000	

Table A7 Total allele frequencies, average number of alleles per locus, and total observed and expected homozygotes and heterozygotes for each marker and population. Dashes represent alleles that were not present at a particular locus for a particular population

Locus/Allele	Population								
	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert
B124									
220	—	0.0161	—	—	—	—	—	—	—
221	—	—	0.0116	—	0.0441	—	0.0119	—	—
222	0.0278	—	—	—	0.0147	—	—	—	0.0333
223	—	—	—	—	0.0294	—	—	0.0385	—
224	0.0139	0.0484	—	—	—	—	—	—	—
225	—	—	0.0233	—	0.0294	0.0152	0.0238	0.0128	—
226	0.0069	0.0161	—	0.0319	—	—	0.0119	—	—
227	0.0139	0.0645	0.1395	—	0.1324	0.1667	0.0952	0.0769	0.0333
228	0.1181	0.1129	0.0349	0.1489	0.0147	—	0.0119	0.0256	0.1000
229	0.0139	—	0.1395	0.0426	0.1176	0.1818	0.1905	0.1282	0.0667
230	0.1875	0.0323	0.1047	0.1383	—	0.0606	—	0.0128	0.1333
231	0.0139	0.0484	0.0698	0.0532	0.0588	0.0152	0.0714	0.0513	0.0667
232	0.0347	0.0645	—	0.0638	0.0294	0.0303	—	0.0128	0.0333
233	0.0347	0.0968	0.3140	0.0638	0.3235	0.3333	0.4643	0.5000	0.1333
234	0.4236	0.3226	0.1047	0.3723	0.0735	—	—	0.0128	0.1667
235	—	0.0161	0.0465	0.0319	0.1029	0.1364	0.1071	0.0897	0.0333
236	0.0694	0.1129	0.0116	0.0426	0.0147	0.0152	0.0119	—	0.1667
237	—	—	—	—	—	—	—	—	—
238	—	—	—	—	—	—	—	—	—
239	0.0069	—	—	—	—	0.0152	—	0.0256	0.0333
240	0.0069	0.0484	—	0.0106	0.0147	—	—	—	—
241	—	—	—	—	—	0.0303	—	—	—
242	0.0278	—	—	—	—	—	—	—	—
243	—	—	—	—	—	—	—	—	—
244	—	—	—	—	—	—	—	—	—
245	—	—	—	—	—	—	—	—	—
246	—	—	—	—	—	—	—	0.0128	—
Hom H _E	16.7692	4.4098	6.8235	8.8387	5.0448	6.0923	11.3373	10.8182	1.2759
Hom H _O	18	13	13	18	7	7	8	12	4
Het H _E	55.2308	26.5902	36.1765	38.1613	28.9552	26.9077	30.6627	28.1818	13.7241
Het H _O	54	18	30	29	27	26	34	27	11

BTERN01

108	—	—	—	—	—	—	—	0.0128	0.0333
109	0.0139	—	—	—	—	—	—	0.0128	—
110	0.0208	—	—	0.0119	0.0294	—	—	—	—
111	0.0347	—	0.0116	—	0.0441	0.0303	—	—	0.0667
112	0.0139	—	—	0.0238	0.0294	—	—	—	—
113	—	—	—	0.0238	—	—	—	—	—
115	0.0139	0.0172	0.0116	0.0357	0.0294	0.0303	0.0357	0.0128	0.1000
117	—	—	—	—	0.0147	—	—	0.0256	—
119	0.0139	0.0172	0.0698	0.0119	0.0294	0.0152	—	—	—
120	—	—	0.0116	—	—	—	0.0119	—	0.0667
121	0.0139	—	—	0.0119	0.0147	—	—	—	—
123	0.0694	0.0345	0.0349	0.0238	—	0.0606	0.0595	0.0256	0.0333
126	—	—	—	—	—	—	—	—	0.0333
128	—	0.0172	—	—	—	—	—	0.0128	—
129	0.0694	0.0690	0.0465	0.0952	0.0294	0.0758	0.0833	0.1282	0.1333
130	—	—	0.0116	—	—	—	0.0119	—	—
131	0.1181	0.0690	0.1279	0.1429	0.0882	0.1818	0.1310	0.1154	0.0333
132	—	0.0172	—	—	—	—	—	0.0128	—
133	0.1875	0.2414	0.1977	0.1786	0.2206	0.1061	0.1667	0.0385	0.2000
134	—	—	—	—	—	—	0.0119	—	—
135	0.1667	0.1552	0.2907	0.1429	0.1176	0.2424	0.1905	0.1923	0.1000
136	—	—	—	0.0119	0.0294	—	0.0238	0.0513	—
137	0.1181	0.1034	0.0116	0.0714	0.1176	0.1212	0.1429	0.1282	0.1000
138	—	—	—	0.0119	—	—	0.0119	0.0128	—
139	0.0417	0.0690	0.0581	0.0714	0.1029	0.0152	0.0119	0.0385	—
148	—	—	—	—	—	0.0152	—	—	—
152	0.0139	0.0172	0.0349	0.0119	0.0147	—	0.0238	0.1667	0.0333
154	0.0903	0.1724	0.0814	0.0952	0.0882	0.1061	0.0595	—	0.0667
156	—	—	—	0.0238	—	—	0.0238	—	—
Hom H _E	7.6993	3.614	6.4588	3.9759	3.2985	4.215	4.5663	4.1948	1.1379
Hom H _O	9	4	11	7	11	8	10	14	4
Het H _E	64.30007	25.386	36.5412	38.0241	30.7015	28.7864	37.4337	34.8052	13.7241
Het H _O	63	25	32	35	23	25	32	25	11
BT10	—	—	—	—	—	—	—	—	—
120	—	—	0.0116	—	—	—	—	—	—
123	—	—	—	0.0122	0.0152	—	—	0.0128	—
125	0.3028	0.2857	0.1977	0.3537	0.1970	0.2879	0.2619	0.2308	0.3667
126	—	0.0357	0.0465	—	0.0303	—	0.0357	0.1026	—
127	0.1056	0.1071	0.0930	0.0976	0.0758	0.1515	0.0595	0.0897	0.1667
128	0.0211	0.0179	—	—	—	—	—	0.0256	—
129	0.1056	0.1429	0.0930	0.2317	0.1667	0.1667	0.1548	0.1026	0.0667

130	0.0282	0.0179	—	—	0.0909	—	—	0.0128	0.0667
131	0.0493	0.0893	—	0.0244	0.0455	0.0606	0.0952	0.0897	—
132	0.0141	0.0179	—	—	—	—	—	—	—
133	0.0070	—	0.0465	0.0122	0.0909	0.0455	0.0238	0.0385	0.0333
134	0.0634	0.0179	0.0233	0.0244	0.0152	—	—	0.0128	—
135	0.0563	0.0536	0.2326	0.0976	0.1515	0.1515	0.1548	0.0897	0.0667
136	0.1408	0.1786	0.1163	0.1220	0.0303	0.0303	0.0238	0.0385	0.1667
137	—	0.0179	0.0349	0.0122	—	0.0152	0.0476	0.0513	—
138	0.0352	—	0.0349	0.0122	—	—	0.0119	0.0128	0.0333
139	0.0141	0.0179	0.0465	—	0.0909	0.0455	0.0833	0.0641	—
140	0.0141	—	—	—	—	—	0.0238	—	—
144	—	—	0.0233	—	—	0.0303	0.0119	—	—
145	0.0211	—	—	—	—	—	—	—	0.0333
147	0.0070	—	—	—	—	—	—	—	—
151	0.0070	—	—	—	—	0.0152	0.0119	0.0256	—
152	0.0070	—	—	—	—	—	—	—	—
Hom H _E	10.0213	4.0364	5.3294	8.3951	3.6615	5.0769	5.5181	3.8442	2.8697
Hom H _O	16	9	17	8	12	3	10	13	5
Het H _E	60.9787	23.9636	37.6706	32.6049	29.3385	27.9231	36.4819	35.1558	12.3103
Het H _O	55	19	26	33	21	30	32	26	10
BL11									
109	—	—	—	0.0122	—	—	—	0.0132	0.0667
119	—	—	—	—	0.0172	—	—	0.0263	—
120	—	—	—	0.0122	—	—	—	0.0132	0.0333
122	0.0211	—	0.0119	0.0122	0.0517	0.0152	—	—	0.0333
123	0.1549	0.2407	0.1548	0.1829	0.1379	0.1818	0.2024	0.2500	0.1667
124	0.0282	0.0370	0.0476	0.0366	0.0345	0.0303	0.0119 0.3214	0.0526	0.0333
125	0.2606	0.2778	0.2619	0.2683	0.2414	0.1061	—	0.2105	0.1667
126	0.0141	0.0185	0.0119	0.0244	—	0.0303	0.0119	—	0.0333
127	0.0563	0.0185	0.0476	0.0366	0.0172	0.0758	0.0476	0.1184	0.0667
128	0.0211	0.0370	0.0119	0.0366	0.0172	0.0758	—	—	0.0333
129	0.0282	0.0370	0.1310	0.0366	0.0862	0.0606	0.1310	0.0921	0.1000
130	0.1690	0.0556	0.0595	0.0976	0.1034	0.0758	0.0595	0.0263	0.1333
131	0.0423	0.0926	0.0476	0.0244	0.0345	0.0909	0.0357	0.0921	—
132	0.1620	0.1296	0.1310	0.1463	0.1897	0.2121	0.0714	0.0658	0.1000
133	0.0352	0.0185	0.0595	0.0244	0.0172	0.0303	0.0952	0.0263	0.0333
134	0.0070	0.0185	0.0119	0.0366	0.0172	0.0152	—	0.0132	—
136	—	0.0185	0.0119	0.0122	0.0345	—	0.0119	—	—
Hom H _E	10.6241	4.1509	5.506	5.5309	3.5965	3.5692	7.2771	5.1733	1.1724
Hom H _O	10	6	12	14	10	5	13	16	4
Het H _E	60.3759	22.8491	36.4824	35.4691	5.4035	29.4308	34.7229	32.8267	13.8276
Het H _O	61	21	34	27	19	28	29	22	11

BL13									
152	0.0486	0.0179	0.0233	—	0.0294	0.0606	0.0119	0.0385	—
154	—	—	—	—	—	—	—	0.0128	—
155	—	—	—	—	0.0147	—	—	—	—
157	—	—	—	—	—	0.0152	—	—	0.0333
158	0.0139	—	0.0116	0.0109	0.0147	—	—	—	0.0333
159	—	—	—	0.0109	—	—	0.0119	0.0256	—
160	0.0347	0.0179	0.0233	0.0109	—	—	0.0119	—	—
161	—	0.0179	0.0349	—	0.0735	0.0606	0.0714	0.1154	0.0333
162	0.1042	0.0714	0.0116	0.0870	0.0147	0.0152	0.0119	—	0.0667
163	0.0139	—	0.1163	0.0109	0.2059	0.1212	0.1310	0.1282	0.0667
164	0.1042	0.1607	0.0116	0.1522	0.0147	—	—	—	0.1667
165	0.1944	0.0714	0.3256	0.1739	0.2794	0.2121	0.2262	0.2821	0.1667
166	0.0903	0.2500	0.0349	0.0978	—	—	—	0.0256	0.1000
167	0.1042	0.1429	0.1395	0.1739	0.1618	0.0909	0.1786	0.1667	0.1333
168	—	—	—	0.0109	—	—	—	—	—
169	0.0625	0.0357	0.1163	0.0652	0.0588	0.1818	0.1548	0.0641	0.1000
170	—	—	—	—	—	—	—	—	—
171	0.0486	0.0536	0.0349	0.0761	0.0294	0.1212	0.0595	0.0256	—
172	—	—	—	0.0326	—	—	—	—	—
173	0.0903	0.0893	0.0465	0.0326	0.0588	0.0606	0.0595	0.0385	0.0667
174	—	—	—	—	—	—	—	—	—
175	0.0278	0.0179	0.0349	0.0435	0.0294	0.0303	0.0476	0.0513	—
176	—	—	—	—	—	—	—	—	—
177	0.0069	0.0179	0.0116	0.0109	0.0147	0.0152	0.0119	0.0256	0.0333
178	—	—	—	—	—	0.0152	—	—	—
179	0.0208	—	—	—	—	—	—	—	—
183	0.0139	—	—	—	—	—	—	—	—
184	—	—	0.0116	—	—	—	—	—	—
185	0.0069	—	—	—	—	—	—	—	—
186	—	0.0179	—	—	—	—	—	—	—
188	—	0.0179	0.0116	—	—	—	0.0119	—	—
190	0.0069	—	—	—	—	—	—	—	—
192	0.0069	—	—	—	—	—	—	—	—
Hom H _E	6.6364	3.2909	6.5176	4.8681	5.1045	3.8	5.4217	5.4026	1.2069
Hom H _O	9	5	9	8	3	3	2	12	2
Het H _E	65.3636	24.7091	36.4824	41.1319	28.8995	29.2	36.5783	33.5974	13.7931
Het H _O	63	23	34	38	31	30	40	27	13
B10									
178	—	—	—	0.0104	—	0.0152	—	—	—
179	0.0486	0.0312	0.0595	0.0312	0.0147	0.0303	0.0476	0.0128	—
180	—	—	—	0.0104	—	—	—	—	0.0333
181	0.0069	—	—	0.0104	—	—	0.0119	0.0128	—
182	0.0069	0.0156	—	0.0104	0.0147	—	—	—	—
183	0.0417	0.0156	0.0476	0.0729	0.1324	0.0152	0.0119	0.0641	0.0333

184	0.0139	0.0312	0.0238	0.0312	0.0294	0.0606	—	0.0128	—
185	0.1528	0.1562	0.2143	0.1042	0.1618	0.0909	0.2262	0.1410	0.3000
186	0.0139	0.0156	—	0.0208	—	0.0758	—	0.0256	—
187	0.1181	0.1250	0.0595	0.0833	0.0588	0.0606	0.1310	0.0641	—
188	—	0.0781	—	0.0938	0.1029	0.1970	—	0.1026	—
189	0.4583	0.3594	0.5119	0.4375	0.3676	0.3030	0.4524	0.4359	0.4667
190	—	—	—	—	0.0147	0.0303	—	—	—
191	0.0556	0.0781	0.0238	0.0312	0.0294	0.0152	0.0476	0.0769	0.1333
192	0.0069	0.0312	—	—	—	—	—	—	—
193	0.0278	0.0469	0.0119	0.0104	0.0294	—	0.0119	—	0.0333
195	—	0.0156	0.0238	—	0.0147	—	0.0119	—	—
196	—	—	—	—	—	—	—	0.0128	—
197	0.0417	—	0.0238	—	0.0294	0.0455	0.0357	0.0385	—
199	—	—	—	0.0312	—	—	—	—	—
201	—	—	—	—	—	0.0606	0.0119	—	—
Hom H _E	18.1748	5.5873	13.0843	10.5684	6.2985	4.8615	11.3735	8.8701	4.5862
Hom H _O	31	13	10	20	10	7	11	12	5
Het H _E	53.8252	26.4127	28.9157	37.4316	27.7015	28.7864	30.6265	30.1299	10.4138
Het H _O	41	19	32	28	24	25	31	27	10
BT28									
174	0.7083	0.4839	0.5476	0.6596	0.5882	0.5758	0.6786	0.6316	0.5333
180	0.2847	0.4839	0.4524	0.3404	0.3676	0.4091	0.3214	0.3684	0.4667
185	—	0.0161	—	—	—	—	—	—	—
186	0.0069	0.0161	—	—	0.0294	0.0152	—	—	—
187	—	—	—	—	0.0147	—	—	—	—
Hom H _E	41.7552	14.2623	20.9398	25.6667	16.1343	16.2154	23.4578	20.08	7.2759
Hom H _O	36	16	20	35	19	17	23	26	7
Het H _E	30.2448	16.7377	21.0602	21.3333	17.8657	16.7846	18.5422	17.92	7.7241
Het H _O	36	28.5079	22	12	15	16	19	12	8
B96									
219	—	0.0156	—	—	—	—	—	—	—
221	0.0139	—	—	0.0104	—	—	—	—	—
222	0.0069	—	—	—	—	0.0152	0.0238	—	—
226	0.0069	—	—	—	—	—	—	—	—
227	0.1042	0.0781	0.0476	0.1354	0.0735	0.1212	—	0.0513	0.2000
228	0.0694	0.0938	0.0714	0.1354	0.0735	0.0606	0.0952	0.0641	—
229	0.0069	0.0156	0.0595	0.0208	—	—	0.0714	—	—
230	0.0069	—	—	—	—	—	—	—	—
232	—	0.0156	—	—	—	—	—	0.0128	—
233	—	—	—	—	0.0147	—	—	—	—
234	—	—	—	0.0104	—	—	—	—	—
235	—	—	—	—	—	—	—	0.0128	—
236	0.0069	—	—	—	—	—	0.0119	0.0128	—

237	—	0.0156	—	—	—	—	—	—	—
238	0.1181	0.0625	0.1548	0.1562	0.0441	0.0606	0.0833	0.1282	0.0667
239	0.0139	0.0156	0.0238	0.0521	0.0588	0.0606	0.0714	0.0385	—
240	0.0486	0.2344	0.1310	0.0104	0.0441	0.0758	0.0714	0.0385	0.0333
241	0.1181	0.1719	0.1548	0.1042	0.1618	0.1364	0.1310	0.2051	0.1333
242	0.0069	0.0156	—	—	0.0147	—	0.0119	0.0256	—
243	0.0347	0.0312	—	0.0208	0.0147	0.0303	0.0238	0.0513	0.0333
244	0.0069	—	—	0.0104	—	0.0152	0.0238	—	0.0333
245	0.2014	0.0938	0.1310	0.0938	0.2353	0.1515	0.1190	0.1282	0.2000
246	—	—	—	0.0312	—	—	—	0.0128	0.0333
247	0.0764	0.0781	0.0833	0.0312	0.1029	0.1061	0.1310	0.0513	0.1000
248	0.0208	0.0156	—	0.0521	0.0294	—	—	0.0128	0.0667
249	0.1111	0.0469	0.1429	0.0729	0.1029	0.1061	0.1190	0.1154	0.0667
250	0.0069	—	—	0.0104	—	—	—	—	—
251	0.0139	—	—	0.0417	0.0294	0.0606	0.0119	0.0385	0.0333
Hom H _E	7.2727	3.4921	4.6386	4.1789	3.7463	2.8615	3.5783	3.6883	1.448
Hom H _O	12	6	7	7	7	2	2	4	2
Het H _E	64.7232	28.5079	37.3614	43.8211	26.9077	30.1385	38.4217	35.3117	13.5517
Het H _O	60	26	35	41	26	31	40	35	13
Mean no. of alleles per locus	14.9 ± 5.5	12.5 ± 3.6	11.3 ± 4.3	13.5 ± 5.4	11.4 ± 4.7	11.1 ± 3.4	11.6 ± 4.4	12.9 ± 4.8	10.7 ± 3.9

Table A8 F_{IS} estimates by locus and population and averaged across locus and population

	Democrat	Boreas	Horseshoe	Evans	Penn	Quail	Niwot	Silverheels	Elbert	All
B124	0.022	0.327	0.172	0.242	0.068	0.034	-0.110	0.042	0.204	0.111
BTERN01	0.020	0.015	0.126	0.080	0.254	0.133	0.147	0.284	0.212	0.141
BT10	0.099	0.210	0.312	-0.012	0.287	-0.076	0.124	0.263	0.193	0.156
BL11	-0.010	0.082	0.180	0.241	0.255	0.049	0.166	0.333	0.210	0.167
BL13	0.036	0.070	0.069	0.077	-0.074	-0.028	-0.095	0.198	0.059	0.035
B10	0.240	0.284	-0.108	0.254	0.135	0.077	-0.012	0.105	0.041	0.113
BT28	-0.192	0.105	-0.045	0.440	0.162	0.047	-0.025	0.333	-0.037	0.088
B96	0.074	0.089	0.064	0.065	-0.059	-0.029	-0.042	0.009	0.042	0.024
All	0.049	0.149	0.110	0.155	0.129	0.025	0.025	0.192	0.127	0.107

Vita

Kaitlyn Marie Whitley grew up with her family in Charlotte, North Carolina. After graduating from West Mecklenburg High School in 2010, she went to the University of North Carolina at Chapel Hill to complete her undergraduate studies. In 2014, she graduated with a double major in Biology and Anthropology and a minor in Environmental Studies. Throughout her undergraduate career, she studied lemurs at the Duke Lemur Center, assisted with animal care and husbandry tasks for big and small cats at the Carolina Tiger Rescue, and studied abroad in Cairns, Australia studying a fragile rainforest ecosystem. After graduating, she went to the Atlantic Rainforest in Paraguay to study Capuchin monkeys and aid in their habituation. She came to Appalachian State University in 2016 and completed her Master of Science degree in Biology in May 2018. Kaitlyn plans to take some time off to travel the world before getting a job in conservation or wildlife biology. Then she hopes to go on to pursue a PhD in Biology in order to continue doing research and ultimately start a career in education.